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Publications Awards 1990–91

National Marine Fisheries Service, NOAA

The Publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publications authored by NMFS scientists and published in the *Fishery Bulletin* volume 89 and *Marine Fisheries Review* volume 52. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles which significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. We offer congratulations to the following authors for their outstanding efforts.

Fishery Bulletin 1991

Thomas A. Munroe
Western Atlantic tonguefishes of the *Symphurus plagusia* complex (Cynoglossidae: Pleuronectiformes), with descriptions of two new species. *Fishery Bulletin* 89:247–287. Dr. Munroe is with the National Systematics Laboratory, Washington DC.

Honorable Mention:

Donald E. Pearson, Joseph E. Hightower, and Jacqueline T.H. Chan
Age, growth, and potential yield for shortbelly rockfish *Sebastes jordani*. *Fishery Bulletin* 89:403–409. Dr. Pearson is with the Tiburon Laboratory of the Southwest Fisheries Science Center, as were Dr. Chan and Dr. Hightower. Dr. Chan has recently retired, and Dr. Hightower is now with the North Carolina State University at Raleigh.

Marine Fisheries Review 1990

Clyde L. MacKenzie Jr.
History of the fisheries of Raritan Bay, New York and New Jersey. *Marine Fisheries Review* 52(4):1–45. Dr. MacKenzie is with the Sandy Hook Laboratory of the Northeast Fisheries Science Center, Highlands, New Jersey. Dr. MacKenzie received Honorable Mention for his 1989 paper on estuarine mollusc fisheries.

Honorable Mention:

Wayne N. Witzell and Edwin L. Scott
Blue marlin, *Makaira nigricans*, movements in the western North Atlantic Ocean: Results of a cooperative game fish tagging program, 1954–88. *Marine Fisheries Review* 52(2):12–17. Dr. Witzell is with the Miami Laboratory of the Southeast Fisheries Science Center as was his co-author, the late Dr. Scott.

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Recent publications in the NOAA Technical Report NMFS Series

108 **Marine debris survey manual**
Christine A. Ribic, Trevor R. Dixon, and Ivan Vining. April 1992, 92 p.

109 **Seasonal climatologies and variability of eastern tropical Pacific surface waters**
Paul C. Fiedler. April 1992, 65 p.

110 **The distribution of Kemp's Ridley sea turtles (*Lepidochelys kempi*) along the Texas coast: An atlas**
Sharon A. Manzella and Jo A. Williams. May 1992, 52 p.

111 **Control of disease in aquaculture. Proceedings of the nineteenth U.S.-Japan meeting on aquaculture, Ise, Mie Prefecture, Japan, 29–30 October 1990**
Ralph S. Svrjcek (editor). October 1992, 143 p.

112 **Variability of temperature and salinity in the Middle Atlantic Bight and Gulf of Maine**
Robert L. Benway, Jack W. Jossi, Kevin P. Thomas, and Julien R. Goulet. April 1993, 108p.

Some NOAA publications are available by purchase from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

Abstract. – Size-specific fecundities of spiny lobster *Panulirus marginatus* were compared for two time-periods: pre- and early exploitation or "before" (1978–81), and post-exploitation or "after" (1991). Fecundity was further evaluated within each time-period at two collection sites that represented the major lobster fishing grounds (Maro Reef and Necker Island) in the Northwestern Hawaiian Islands. Complementary data on egg size and spawning-frequency index were compared between study sites and time-periods.

Study sites and time-periods had no observable effects on egg size or spawning frequency, and there was no temporal effect on fecundity at Maro Reef. Fecundities at the two sites differed, however; "after" size-specific fecundity was an estimated 16±9% greater than "before" fecundity at Necker Island. Observations suggest that the recent increase in fecundity at Necker Island may reflect a compensatory (density-dependent) response to greater exploitation at this site. Results are discussed in terms of evidence for density-dependent responses in other, exploited spiny lobster stocks.

Manuscript accepted 19 August 1992.
Fishery Bulletin, U.S. 91:1-7 (1993).

Comparisons of spiny lobster *Panulirus marginatus* fecundity, egg size, and spawning frequency before and after exploitation

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The spiny lobster *Panulirus marginatus* (Quoy & Gaimard) is endemic to the Hawaiian Archipelago and Johnston Island (Brock 1973, Uchida et al. 1980). This species supported a major commercial fishery in the main Hawaiian Islands (MHI) prior to the rapid increases in demand after World War II (Uchida et al. 1980). Not until the expansion of the fishery into the Northwestern Hawaiian Islands (NWHI) began in 1977 did the species again support a valuable commercial enterprise, complemented with bycatches of slipper lobster *Scyllarides squamosus* (H. Milne-Edwards) and *S. haanii* (De Haan). A fishery management plan was created in 1983 to regulate the fishery based on minimum size limits and limited entry.

Prior to 1990, annual landings averaged 1–2 million spiny lobster worth US$4–6 million ex-vessel. Beginning in 1990 and continuing until the fishery closure in early 1991, however, landings fell heavily, equaling one-fifth of the long-term average (Landgraf 1991). These decreases reflected real declines in abundance, as both research and commercial catch per trap-haul (CPUE) similarly declined (Landgraf 1991). The present belief is that recent declines in the spiny lobster CPUE reflect a combination of continued, heavy exploitation and the occurrence of a series of poor year-classes, particularly at Maro Reef, one of the two major NWHI fishing grounds (Polovina 1991).

Recent research by Polovina (1989) has indicated that a density-dependent decrease in the size-at-onset of egg production occurred in NWHI spiny lobster from 1977 to 1986–87. Additional types of compensatory responses to lower population densities may be operative and may have a major influence on the dynamics of these lobster populations, but data are lacking (Polovina 1989). Included among these compensatory mechanisms is an increase in size-specific fecundity, a phenomenon suggested for other species of spiny lobsters (Chittleborough 1976 and 1979, Beyers & Goosen 1987, MacDiarmid 1989).

With the *a priori* prediction that size-specific fecundities might have increased for NWHI spiny lobster

during the recent period of low population densities, we initiated a study of its fecundity and related reproductive life history. Prior to our study, little quantitative information existed on the fecundity of this species, and data were limited to the waters off Oahu in the MHI (Morris 1968, McGinnis 1972). Our objective is to compare the size-specific fecundities of NWHI spiny lobster between two time-periods: an early or pre-exploitation (hereafter referred to as "before") period in 1978–81, and a postexploitation ("after") period in 1991, when population densities had declined to a fraction of their pre-exploitation level.

Methods and materials

Specimen collection

Spiny lobster were collected using baited commercial traps at Maro Reef and on the offshore bank of Necker Island, the second of the two major NWHI fishing grounds (fig. 1, Polovina 1989). Lobsters were trapped during multiple cruises aboard chartered commercial vessels and the NOAA ship *Townsend Cromwell* during the summertime (May–August) breeding seasons of 1978–81 (the "before" period) and on a single cruise by the *Townsend Cromwell* during June–July 1991 ("after"). Commercial traps fished for a standard (overnight) soak period were used at each site during both time-periods. Specimens were similarly handled aboard the chartered vessels and the *Townsend Cromwell*.

Sample processing

Lobsters were sexed, carapace length (CL) measured, and the egg developmental stage of egg-bearing ("berried") females scored as either Stage 1 (orange = freshly extruded), Stage 2 (brown = late development), or Stage 3 (white = hatching imminent). The CL, defined as the distance along the middorsal line from the transverse ridge between the supraorbital spines to the posterior margin of the carapace, was measured to the nearest 0.1 mm. Berried female specimens were either processed fresh in the ship's wet lab or flash-frozen (damp) aboard ship for processing ashore.

In the laboratory, brood sizes were estimated using Stage-1 females whenever possible so as to minimize the effect of potential egg loss (Morgan 1972, Annala & Bycroft 1987). The eight pleopods including egg clusters (setae bearing the egg masses) were separated by dissection and placed on absorbent paper towels. Egg clusters were then stripped off the pleopods onto preweighed weigh boats. Each individual female's total egg complement was weighed (damp weight to 0.1 mg) and then reweighed following determination of egg subsample weights; these two weighings were then averaged to provide a measure of the total egg mass. Random subsamples comprising a minimum (by weight) of 1% ($\bar{x}$=1.5%) of the female's total egg mass were weighed (0.1 mg) and later enumerated to estimate fecundity (F_t=total number of eggs) by proportion:

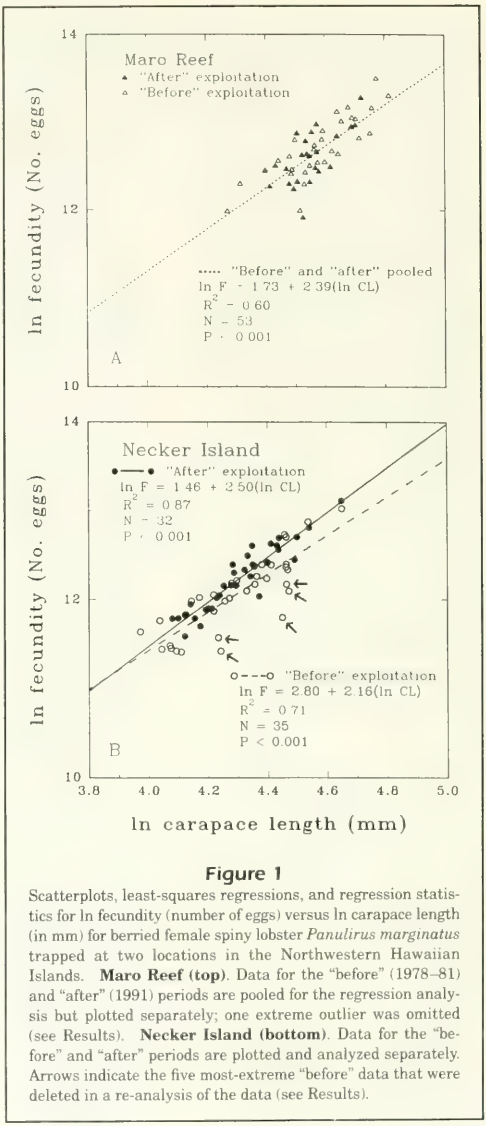

Figure 1

Scatterplots, least-squares regressions, and regression statistics for ln fecundity (number of eggs) versus ln carapace length (in mm) for berried female spiny lobster *Panulirus marginatus* trapped at two locations in the Northwestern Hawaiian Islands. **Maro Reef (top)**. Data for the "before" (1978–81) and "after" (1991) periods are pooled for the regression analysis but plotted separately; one extreme outlier was omitted (see Results). **Necker Island (bottom)**. Data for the "before" and "after" periods are plotted and analyzed separately. Arrows indicate the five most-extreme "before" data that were deleted in a re-analysis of the data (see Results).

$$F_t = F_s \cdot \left(\frac{W_t}{W_s}\right),$$

where F_s = number of eggs in subsample, W_s = weight of egg subsample, and W_t = total weight of eggs. Some frozen-thawed egg masses were fixed in 4% formaldehyde for 1 month to harden eggs prior to weighing and counting. A single subsample was used to characterize the fecundity of each "before" specimen. Three replicate subsamples were used to estimate the sampling error of "after" fecundity determinations; the three pooled subsamples provided the best estimate of "after" fecundity. Total eggs were counted for one of the "after" specimens to gauge the accuracy of the weighing and counting procedures.

Egg sizes were estimated to complement the fecundity data. For a subset of both "before" and "after" Stage-1 specimens, a minimum of 25 eggs per female were randomly chosen and measured (random axis, at 50×) using a dissecting microscope with calibrated eyepiece micrometer.

Total egg production is the product of the number of eggs produced per spawning (brood size) and the number of spawnings. For females above threshold body sizes at onset of egg production at each of the sites during the two time-periods (Polovina 1989), we indexed spawning frequency based on the relative frequencies of berried (to total) females present in historical catch data of the Honolulu Laboratory. We used records of catches made at Maro Reef and Necker Island on summertime cruises during years within pre- and postexploitation periods when sufficient data were available (1977, 1988–91).

Statistical analysis

Analysis of covariance (ANCOVA, SAS Proc GLM; SAS 1985) was used to compare mean fecundities between sampling periods; CL was used as a covariate to adjust for potential body-size differences between periods. As justified, central tendencies in fecundity were compared between periods ("before," "after") using least-square means (LSM) and their standard errors (SEM). Period and site (Maro Reef, Necker Island) were evaluated as class variables. Student's *t*-test, with degrees of freedom adjusted (as necessary) by Satterthwaite's approximation for unequal variances (Bailey 1981), was used to compare indices of spawning frequency between periods.

Results

Size-fecundity relationships

Paired CL and fecundity data were available for 54 spiny lobster from Maro Reef. At Necker Island, there were 67 analogous data pairs (Appendix A). Over 90% of the "before" specimens had Stage-1 eggs, and Stage-2 eggs were equally distributed among specimens from the two sites. Incidence of Stage-2 eggs appeared higher in the "after" samples from Maro Reef (8/24=33%) than in the analogous samples from Necker Island (3/32=10%). No lobsters with Stage-3 eggs were collected during either time-period. The coefficient of variation [CV=(SD/$\bar{x}$)·100] of the triplicate "after" fecundity estimates was about 2%. The accuracy of the mean of the two weighings of an entire egg mass was within 4% of a total count.

At Maro, slopes were indistinguishable between periods, regardless of whether an obvious outlier (whose residual deviated 8.5% from its predicted value) was included (ln CL × period interaction: $F_{1,50}=0.06$, $P=0.81$) or was deleted from the analysis ($F_{1,49}\leq 0.01$, $P>0.99$). Slopes also were indistinguishable between the two periods at Necker Island ($F_{1,63}=1.17$, $P=0.28$).

Intercepts did not differ between periods at Maro Reef ($F_{1,50}=0.22$, $P=0.64$), but the period (intercept) effect at Necker Island was significant ($F_{1,64}=10.17$, $P=0.002$). Greater size-specific fecundity in the "after" period at Necker Island persisted, even if the five most-extreme "before" values (noted by the arrows in Fig. 1) were deleted and the analysis rerun ($F_{1,59}=4.40$, $P<0.05$). Using all available data, the power (1 minus Type-II error) of the test for period differences at Necker Island was 84%, for a critical Type-I error of 5% ($\alpha_2=0.05$).

CL significantly influenced fecundity at both Maro Reef ($F_{1,50}=70.6$, $P<0.001$; Fig. 1) and at Necker Island ($F_{1,64}=215.6$, $P<0.001$; Fig. 1). After adjustment for period differences in CL, the fecundity of lobsters at Necker Island was an estimated 16±9% greater during the "after" versus the "before" period (LSM±SEM of lnF = 12.224±0.034 and 12.072±0.033, respectively). Unlike the case at Necker Island, mean fecundity at Maro Reef differed only by <3% between the "before" and "after" periods (LSM±SEM = 12.680±0.041 and 12.651± 0.046, respectively).

Egg size

The median egg diameters of 22 females collected from Maro Reef and Necker Island during the "before" period were 0.58–0.69 mm. The analogous data for 53 "after" females were 0.61–0.73 mm, with a grand median of 0.66 mm.

Slopes of female body size/egg size (median diameter) relations were indistinguishable between sites (CL × site interaction: $F_{1,51}=0.55$, $P=0.46$). Intercepts also were indistinguishable: egg size was uninfluenced by site ($F_{1,52}=2.75$, $P=0.10$). Carapace length had no

effect when sites were evaluated separately ($F_{1,52}$=0.11, P=0.75). However, female size significantly but weakly (R^2=0.08) affected egg size when data for the two sites were pooled (CL effect: $F_{1,53}$=2.104, P=0.04; median egg diameter = 30.2 EPU+0.039 CL_{mm}; N=55; EPU= 0.0197 mm).

Spawning frequency

The relative frequency of berried/total adult females collected at Maro Reef and Necker Island during the summer of 1988 (N=3085 adult females), 1990 (1198), and 1991 (1165) was 0.246±3.401 ($\bar{x}$±1SD, N=6 site-year combinations). This index of the spawning frequency of females did not differ (t'=0.01, P>0.9) from 0.230±0.510, the estimated frequency for 3037 females collected during the summer of 1977 (N=2 site-years).

Discussion

Fecundity-body size relations

Exponents of the curvilinear, $F=a \cdot CL^b$, relations observed in this study ranged from 2.16±0.241 (statistically equal to 2.0) to 2.50±0.175 (2.0<b<3.0; Fig. 1). Perhaps both area of egg-bearing surface and volume (female body mass) influence fecundity in this species. Prior data on size-specific fecundity for an Oahu population of *P. marginatus* allow us to estimate the exponent in the equation $F=a \cdot CL^b$ as 2.96±0.31SE (N=11; table XV, Morris 1968).

A variety of linear:cubic relationships are available for other spiny lobster species. The following values of the exponent b in the power equation are either known or calculable for: *Panulirus interruptus* (1.0, Lindberg 1955), *P. homarus* (1.0, Berry 1971), *P. cygnus* (1.0, Morgan 1972); *Jasus verreauxi* (1.0, Kensler 1967), *J. edwardsii* (1.0, Kensler 1968; 3.01, McDiarmid 1989; 2.11–3.75, Annala & Bycroft 1987), *J. lalandii* (1.0, Beyers & Goosen 1987 and Pollock 1987; 3.58, Zoutendyk 1990), *J. tristani* (1.0, Pollock & Goosen 1991), *Nephrops norwegicus* (2.35, Thomas 1964 in Aiken & Waddy 1980). Best fits thus vary from linear to cubic both among species and among geographic populations within species. The only apparent pattern is the generally linear relationship between length and egg number in other *Panulirus* spp.

Parameter interrelations

Although size-specific fecundity clearly changed between the "before" and "after" periods of exploitation for Necker Island lobster, neither egg size nor spawning frequency appeared to differ between the two sampling periods at either study site. Theoretically, size-specific fecundity might be expected to co-vary with egg size and spawning frequency (Gadgil and Bossert 1970). However, in many organisms, offspring size and number often do not track one another simultaneously or to an equivalent extent (Capinera 1979, Roff 1982). Therefore, our observation that egg size did not co-vary with egg number in *Panulirus marginatus* should not be surprising. Perhaps strong selection for planktonic larvae of relatively invariant body size is typical within particular populations of spiny lobster, even though average egg sizes might differ among populations of some species. This speculation is consistent with our observation that estimated egg volume varied only about 50% among female *P. marginatus* of a large range of body sizes from either site. This value is low compared with those of most marine teleosts (Bagenal 1971).

Site and period comparisons

The site (geographic population) differences observed in this study of NWHI spiny lobster are not without precedent in other spiny lobsters. Annala & Bycroft (1987) and Beyers & Goosen (1987), for example, observed geographic differences in the size-specific fecundities of *Jasus edwardsii* and *J. lalandii*, respectively. For *J. edwardsii*, differences in size-specific fecundity were detected for populations ranging from extreme southern to northern New Zealand (Annala & Bycroft 1987). The spatial scale of the geographic pattern noted by Beyers & Goosen (1987) for *J. lalandii* was 600 km. Approximately 650 km separate Necker island and Maro Reef.

Unlike the Necker Island population, the fecundity of lobsters from Maro Reef was indistinguishable between the two sampling periods. The absence of a period effect at Maro Reef was not due to larger variance at a similar effect size (Cohen 1988); rather, the standard deviation of the residuals of lnF at Maro Reef (0.217) resembled that for Necker Island (0.206). There is the possibility, though, that size-specific fecundity has increased at Maro Reef too, but we were unable to detect it because of an artifact that particularly affected the fecundity estimates of "after" specimens from this site. Many of our "after" specimens from Maro Reef had Stage-2 eggs. Greater egg loss might have occurred during the handling of these specimens, because eggs at later stages of development may be more prone to dislodgement (Annala & Bycroft 1987). Anecdotal observations of the integrity of egg masses of the "after" females from Maro Reef suggest that, even though some additional egg loss might have occurred, it is unlikely to have been sufficient to obliterate an increase in size-specific fecundity of a magnitude similar to that observed for Necker Island lobster.

A significantly greater size-specific fecundity persisted at Necker Island in the "after" period even if the most-likely outliers from the "before" data were excluded from the analysis. This conservative re-analysis strongly suggests that period differences in the size-specific fecundities of Necker Island lobster are real. The magnitude of our best estimate of this difference (16%) further suggests that it represents a biologically meaningful change. A much more extensive series of before-and-after data would be necessary to resolve this issue beyond a reasonable doubt.

On balance, then, our data suggest that the size-specific fecundity of NWHI spiny lobster has increased at Necker Island, but likely not at Maro Reef, following a decade of heavy exploitation at both fishing grounds. Why and how can this be?

The data of Polovina (1989) suggest one possible explanation. The density-dependent decrease in mean carapace length-at-onset of egg production has been proportionately greater for female lobsters at Necker Island (10–15%, 67.8 to 57.9–60.8 mm) than at Maro Reef (6–9%, 74.8 to 68.2–70.5 mm; table 3, Polovina 1989). In 1977, the pre-exploitation densities (catch per trap-haul) of adult lobsters were higher at Necker Island ($\bar{x}$±SEM = 5.76±0.75) than at Maro Reef (3.89±0.45); yet by 1986–87, densities had declined more at Necker Island (to 2.14±1.24) than at Maro Reef (2.65±0.67; tables 1&2, Polovina 1989). By decreasing densities to a greater extent (thereby making more shelter or food resources available per lobster), it is possible that the effects of more intense cropping may now extend beyond decreased size-at-maturity to greater size-specific fecundity for Necker Island lobster.

Other factors besides exploitation might be somehow influencing the density and size-specific fecundity of *P. marginatus* at Maro Reef. Relatively few small lobsters were present at Maro Reef compared with Necker island during either of the time-periods used in our fecundity comparison (Polovina 1989; Fig. 1). Even so, disproportionately low recruitment at Maro Reef during 1986–88 might have recently exaggerated long-term baseline differences in the body-size distributions of exploitable *P. marginatus* at the two banks (Polovina & Mitchum 1992). Of the several possible reasons for higher pre-exploitation densities at Necker Island (more productive bottom habitat, fewer adult lobster predators), none is presently substantiated. Studies are in progress to evaluate the quality and distribution of bottom habitats among Maro Reef, Necker Island, and other NWHI lobster grounds.

Density-dependent reproduction in lobsters

Density-dependent changes in egg production have been described or suggested for several other species of spiny lobster. Examples include changes in the number of spawnings (duration of spawning season) for individual females (Chittleborough 1976, 1979) as well as increases in size-specific fecundities (Thomas 1964, Beyers & Goosen 1987, MacDiarmid 1989) in response to lower population densities or otherwise greater food availabilities. Body size at onset of sexual maturity has responded in qualitatively different fashion to changes in lobster densities among different populations and species of lobsters. Several studies of *Jasus lalandii* (e.g., Pollock & Goosen 1991) have observed smaller body sizes at first maturation in stunted or physiologically stressed, high-density populations. As mentioned previously, Polovina (1989) has demonstrated the opposite response to reductions in adult densities resulting from exploitation. A fundamental, biological difference is whether size-at-maturity is an age- or size-dependent trait for a particular species and population. It is reasonable to expect species differences in the determination of maturation, and comparative studies of the mechanisms regulating the onset of maturation in different spiny lobsters would be informative.

Statistical considerations

Several studies have evaluated, but been unable to detect, geographic variations in fecundity (Thomas 1964, Morgan 1972). The study by Morgan (1972) represents a case in which sample sizes were small and power was low despite nontrivial effect sizes. Future studies of lobster fecundity should report statistical power, especially when tests are unable to reject null hypotheses of no difference among populations.

Acknowledgments

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Appendix A

Body size (carapace length, CL mm) and fecundity (F, no. eggs $\times 10^3$) data for individual spiny lobster *Panulirus marginatus* collected during "before" and "after" exploitation periods at Necker Island and Maro Reef. Data are ordered by increasing CL within period at each site.

Maro Reef				Necker Island			
Before		After		Before		After	
CL	F	CL	F	CL	F	CL	F
71.5	161	81.3	262	53.1	113	59.1	134
74.7	220	82.6	222	56.7	128	60.3	134
85.0	286	84.2	284	57.0	93	61.6	110
88.3	300	87.4	271	58.6	97	61.6	138
88.8	246	88.2	223	58.8	94	62.8	157
89.0	258	89.6	212	59.9	91	63.7	134
89.9	363	90.6	399	60.9	90	64.9	124
91.4	162	90.7	230	61.8	137	66.1	148
92.8	219	92.2	309	63.0	160	66.6	148
93.1	250	92.4	157	64.7	167	67.5	147
94.5	270	93.3	367	67.9	172	68.6	169
95.9	325	93.7	318	67.9	143	69.2	174
96.1	341	94.5	308	68.9	106[b]	70.2	192
96.8	316	94.6	231	69.5	91[b]	72.0	196
97.1	280	95.2	407	70.5	160	72.4	243
98.5	364	96.4	269	71.6	166	72.7	226
98.8	402	96.8	438	72.1	196	73.2	194
99.4	282	97.1	108[b]	73.4	202	75.3	232
101.9	319	97.5	260	75.9	180	76.1	273
103.7	499	101.4	275	77.8	238	76.8	216
104.0	308	103.7	382	78.0	194	77.3	303
105.2	448	108.9	433	78.5	212	77.4	251
107.6	525	110.2	442	79.8	242	79.1	172
109.0	467	112.4	595	81.2	207	81.4	250
110.3	460			82.4	241	82.3	308
111.6	370			85.6	133[b]	84.0	303
115.7	391			86.3	339	84.5	285
116.4	522			86.6	235	84.6	328
118.2	730			86.7	330	89.2	258
123.2	601			86.7	243	90.0	336
				86.8	194[b]	93.7	368
				87.2	228	104.5	499
				87.5	179[b]		
				93.4	390		
				104.6	454		

[a]Extreme outlier deleted from final analysis.
[b]One of five most-extreme values deleted from conservative re-analysis (see Results).

Spawning time, growth, and recruitment of larval spot *Leiostomus xanthurus* into a North Carolina estuary

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Abstract.—Larval spot *Leiostomus xanthurus* were sampled weekly as they recruited to the Newport River estuary near Beaufort Inlet, North Carolina to determine their density, and age and size composition. Density data and otolith age distributions were used to calculate the relative contribution of birthweek cohorts to the seasonal recruitment of spot larvae. The protracted 1987–88 spawning season extended from mid-October to mid-March, with 90% in a 2-month period beginning mid-November. Larvae were recruited to the estuary over 5 months at a mean age of 82 d and mean standard length of 17.2 mm. Smaller, younger larvae generally immigrated to the estuary early (December–January) and late (late April), while larger, older larvae immigrated during the interim peak recruitment period (February to mid-April). In any recruitment week, larvae were from 2–10 birthweek cohorts, but recruitment was strongly influenced by the number of larvae of the dominant cohorts.

Larval spot were also sampled in the ocean between Cape Fear and Oregon Inlet off North Carolina to determine their distribution, abundance, and size and age composition. Age and size of larvae were inversely related to distance from shore. Highest densities of larvae were generally found outside the 30 m isobath. Distribution data supported the hypothesis that spot spawned south of Cape Hatteras on the outer continental shelf contribute to recruitment in Chesapeake Bay. A Kolmogorov-Smirnov test did not demonstrate a significant difference between birthdate distributions for ocean and estuarine larvae. This implied that mortality was not age-specific for larvae collected at different times. A Laird-Gompertz growth equation fit to age and size data for larvae collected in the ocean and estuary predicted that they grew from 1.2 mm at hatching to 16.1 mm in 80 d.

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Fishery Bulletin, U.S. 91:8-22 (1993).

Spot *Leiostomus xanthurus* is distributed from the Gulf of Maine to the Bay of Campeche, Mexico. The area of greatest abundance and the center of the commercial fishery on the Atlantic Coast extends from Chesapeake Bay to South Carolina (Johnson 1978, Mercer 1989). Spot spawn offshore during the fall and winter, and their larvae immigrate to nursery areas in estuaries (Hildebrand & Cable 1930, Fahay 1975, Chao & Musick 1977, Warlen & Chester 1985). Historically, spot have been among the most important commercial and recreational fishes in North Carolina (Miller et al. 1984, Mercer 1989). Hettler & Chester (1990), Warlen & Burke (1990), and Warlen (unpubl. data) have shown that larval spot are consistently the most abundant of the fall/winter spawning species whose larvae are found in Beaufort Inlet, North Carolina. The abundance of this species is probably a function of the relatively high densities of larvae that recruit into estuaries over an extended period of several months. Recruitment is defined as the movement (immigration) of spot larvae from the ocean into the lower estuary.

There have been studies on the early life history of spot regarding development (Fruge 1977, Fruge & Truesdale 1978, Powell & Gordy 1980), feeding (Govoni et al. 1983, 1985), distribution and abundance (Lewis & Judy 1983, Warlen & Chester 1985, Sogard et al. 1987), metabolic responses to cold (Hoss et al. 1988), and age and growth (Beckman & Dean 1984, Warlen & Chester 1985, Siegfried & Weinstein 1989). Although Beckman & Dean (1984) determined the relationship between spawning and part of the estuarine recruitment period, no studies have estimated the relative contribution of age (birthweek) cohorts to the number of estuarine recruits, or the seasonal changes in relative abundance of larvae that survive to reach the estuary. Such studies require systematic, quantitative sampling of larvae newly recruited to the estuary in order to estimate within-season relative abundances. Also, they require age determination of larvae throughout recruitment.

The density of larvae recruited from each birthweek gives an estimate of the spawning-date distribution of spot which can be compared with similar distributions determined from either offshore egg production (although these are difficult to obtain) or younger larvae caught off-

shore. If cohort survival is similar, the birthdate distributions would not be expected to differ. Age of larvae recruited to the estuary is a useful measure of the transport period from offshore spawning to recruitment into the estuary. Transport time may be expected to vary seasonally as a function of transport rate and spawning distance from shore (transport distance).

The objectives of this study were to (1) determine age and size of spot larvae immigrating into the Newport River estuary through Beaufort Inlet, (2) estimate the spawning season (back-calculated from ages of recruited larvae) and the relative contribution of birthweek cohorts to the total larval spot recruitment, (3) relate the density, age and size distributions, and back-calculated birthweeks of spot larvae collected off the North Carolina coast to the same cohorts collected later just inside the mouth of the estuary, and (4) estimate the growth rate of larvae.

Methods

Spot larvae used in this study were collected in both marine and estuarine areas. A 1×2 m neuston net frame with a 945 μm mesh net (Hettler 1979) was used to collect larvae (some specimens were early juveniles) at a station adjacent to Pivers Island in the lower Newport River estuary about 2 km inside Beaufort Inlet (Fig. 1). The fixed net was fished, with the top of the frame just under the water surface, from a bridge platform in the center of the channel. A flowmeter (General Oceanics model 2030) was attached to the mouth of the net to estimate the amount of water sampled. Four consecutive sets were made during nighttime hours at mid-flood tide, when current was the strongest. Because of the expected seasonal variation in larval fish densities, sets were 2–8 min long ($\bar{x}$=5 min) and sampled 58.4–443.0 m^3 of water. Samples were collected weekly from 10 November 1987 to 4 May 1988. The mean of data from all sets on a given night was used as the estimate of density of spot larvae.

Sampling for spot larvae was also conducted off the North Carolina coast from Cape Fear to Oregon Inlet (Fig. 1) during two phases (12–13 January and 2–5 February) of cruise 172 of NOAA ship *Oregon II* in 1988. Sampling stations were arranged along a transect from Beaufort Inlet approximately south-southeast to the 400 m isobath, then along the Gulf Stream to about 36° N latitude, and finally inshore along a transect toward Oregon Inlet (Fig. 1). Additional stations along bands parallel to the coast were added in February in Onslow Bay. Samples at a station were obtained from either a day or night oblique plankton tow using a 60 cm Bongo frame fitted with 333 and 505 μm mesh nets and rigged with flowmeters. The amount of water filtered on a tow was depth-dependent and varied between 72.4 and 476.8 m^3. Ichthyoplankton samples from both estuarine and marine areas were preserved in 95% ethanol. Spot larvae from each sample were counted and density estimated as larvae/100 m^3.

Larval spot were randomly sampled from each estuarine collection for aging. If the total number of larvae in a collection was ≤20, then all fish up to a maximum of 10 were used. If there were more than 20 specimens in a collection, then 10–40 larvae were taken for the sample depending upon the coefficient of variation (CV) of the standard length (SL) of 20 fish. If CV was 0.10–0.12, a subsample of 20 fish was taken. If CV was >0.12, the subsample was 30 fish, except when more than 1000 fish were caught, at which time 40 fish were used. Larvae were measured to the nearest 0.1 mm SL. Age was determined according to the method of Warlen & Chester (1985). The estimated age of a larva was the observed number of sagittal growth increments from one reading plus the estimated number of days from hatching to first increment formation (5 d). The precision in duplicate readings of otoliths from 25 larvae (range 32–86 d) was estimated from the differences in paired readings. The mean (±SD) difference was 1.52±1.26 growth increments, and the range was 0–4 increments. The birthdate (= spawning date) of each larva was back-calculated by subtracting its estimated age from the date of capture. Larvae spawned in a given calendar week were considered in the same calendar birthweek cohort. The spawning period of spot was estimated from the back-calculated birthdates of larvae recruited to the estuary over all seasons. For each weekly collection, the percentage of larvae from each birthweek cohort was determined. Each percentage was multiplied by the corresponding weekly density total (larvae/100 m^3) to give the density of larvae from each birthweek cohort. The densities for each birthweek cohort were summed over all collections and their percentage contribution to the total density (1540 larvae/100 m^3) for all birthweek cohorts was calculated. The Laird version (Laird et al. 1965) of the Gompertz growth equation was used to describe growth of spot larvae from the combined marine and estuarine collections. To stabilize the variance of length over the observed age interval, we used the log-transformed version of the Gompertz growth equation.

Results

Estuarine abundance and age/size distribution of larvae

Abundance of larvae A total of 9760 spot larvae was collected at Pivers Island between 2 December 1987

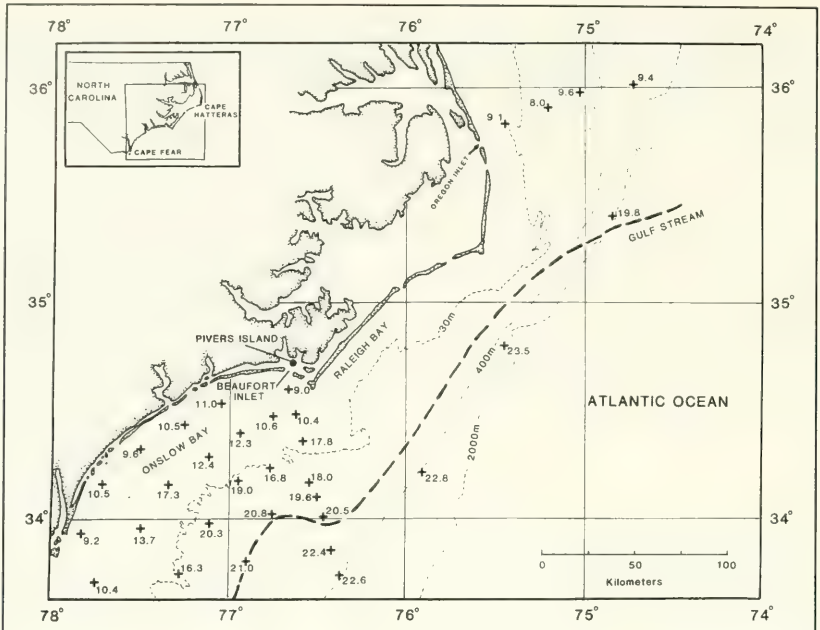

Figure 1

Location of sampling sites for spot *Leiostomus xanthurus* larvae at Pivers Island near Beaufort Inlet and ocean stations ("+") off the North Carolina coast. Surface-water temperatures are indicated for February 1988 stations.

and 4 May 1988 (Fig. 2). The 4th of May was considered the virtual end of the recruitment period, since spot densities had declined to <2 larvae/100 m^3 over the last 2 weeks of sampling. The sum of the weekly mean larval densities over all collections (1540 larvae/100 m^3) was used as the basis for determining the percentage of recruited larvae from each birthweek cohort. Larval density gradually increased during the first 10 weeks of sampling, varying from 0 to 40 larvae/100m^3 ($\bar{x}$=14.6). Approximately 9% of the larval spot recruitment occurred during this period. The period of highest density ($\bar{x}$=138.3 larvae/100 m^3) occurred during 10 February–13 April, when 88% of the larvae were recruited to the estuary. During this 10-week period, there was wide variation in relative abundance with four clear peaks, the largest occurring on 23 March when 34% of all larvae were collected. During the last 3 weeks of sampling, larval density declined to very low levels ($\bar{x}$=3.7/100 m^3) and represented less than 3% of the total spot larvae collected. There was variation in the catch densities among net sets on any given sampling night. Excluding the first 4 weeks when no spot larvae were collected in 41% of the sets, the average nightly coefficient of variation was 65.3% (range 20.3–119.5%).

We assumed that larvae caught each week were newly recruited to the estuary and that they were in transit to upper reaches of the estuary past Pivers Island. These assumptions are supported by the generally small standard error in the age of larvae within each collection (Fig. 3). The small observed within-sample variation in age is probably due in part to mixing of age cohorts in the ocean prior to estuarine recruitment. Since larvae were not accumulating in the lower estuary, there was no increase in standard error of mean age over time. Also, in the week following each of the four peaks (Fig. 2) densities were relatively low, a pattern that did not suggest substantial carryover of fish from week to week.

Age and length of larvae The weekly mean age of spot larvae caught at Pivers Island fluctuated between

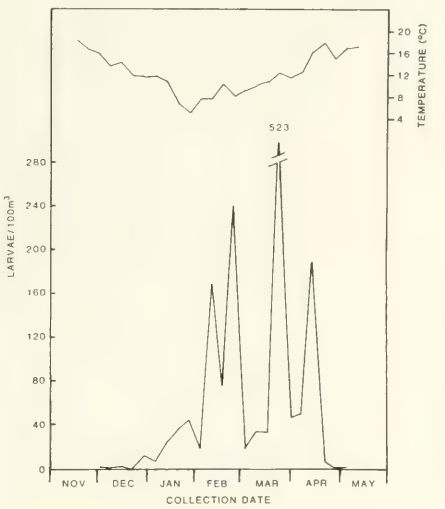

Figure 2

Weekly mean density (larvae/100 m^3) of spot *Leiostomus xanthurus* larvae in collections at Pivers Island in the Newport River estuary, November 1987 to May 1988 (no larvae caught before 2 December). Mean weekly surface-water temperature calculated from hourly measurements at Pivers Island.

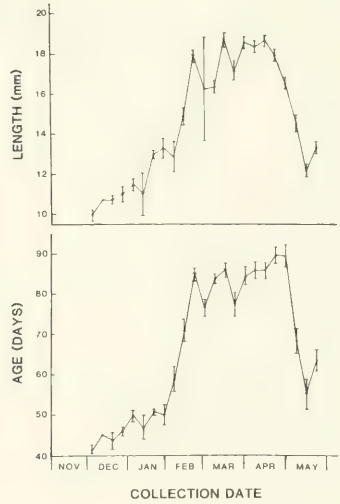

Figure 3

Mean standard length (mm±1SE) and age (d±1SE) of spot *Leiostomus xanthurus* larvae collected weekly, November 1987 to May 1988, at Pivers Island in the Newport River estuary (no larvae caught before 2 December).

37 and 108 d, ($\bar{x}$=82.4 d); weekly mean SL varied from 9.2 to 22.2 mm ($\bar{x}$=17.2 mm). The weekly mean age and SL of spot larvae (Fig. 3) increased from the beginning of the recruitment period, when the youngest and smallest larvae were caught, to the beginning of the period of peak recruitment density (10 February). Thereafter, average values remained high, only decreasing during the last 3 weeks. The age and size distributions of all spot larvae recruited to the estuary (Fig. 4) indicated that 68% were between 75 and 95 d, and 80% were between 15.1 and 20.0 mmSL. The mean age (±SE) and SL (±SE) of larvae corresponding to the three recruitment periods of different densities were 50.4 (±2.7), 84.6 (±1.4), and 62.6 d (±3.8), and 11.8 (±0.49), 17.7(±0.31), and 13.4 mm (±0.69).

Spawning time Spawning, which was continuous over a 5-month period, began near mid-October and ended about mid-March (Fig. 5). Over 99% of spawning occurred from 1 November to 24 January (22 weeks). Only about 1% was contributed by 9 weekly cohorts: 2 before and 7 after the main spawning period. Cohorts from 22 November to 10 January contributed >80% of total larvae (Fig. 5). The midpoint in spawning was the week of 20 December.

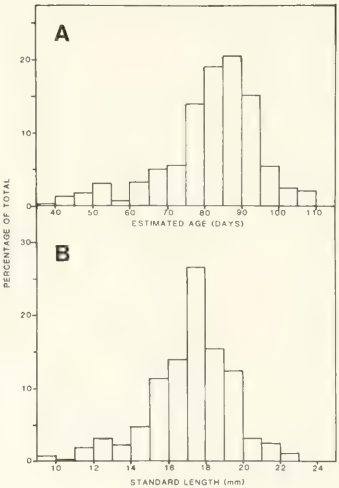

Figure 4

Percentage distribution of larval spot *Leiostomus xanthurus* recruited to the Newport River estuary, November 1987 to May 1988, by **(A)** estimated age (5d intervals) and **(B)** standard length (1 mm intervals).

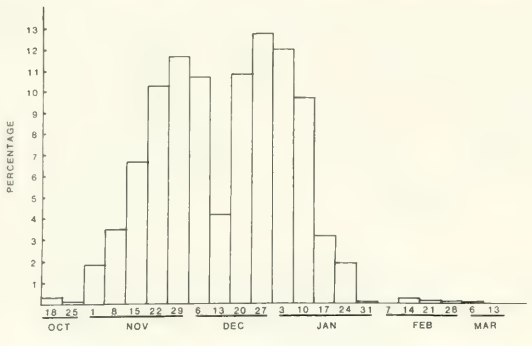

Figure 5

Percentage distribution of the number of larval spot *Leiostomus xanthurus* of back-calculated birthweeks recruited to the Newport River estuary, November 1987 to May 1988.

Age and length of birthweek cohorts Larvae from the beginning and end of the spawning period reached the estuary at younger mean ages than those from the middle period (Fig. 3). Larvae from birthweek cohorts were recruited to the estuary over periods ranging from 2 to 10 weeks, with an average of 7 weeks for the main spawning period (Table 1). In all but four cohorts (25 October, 22 November, 6 December, and 3 January), at least 50% of the larvae from the cohort reached the estuary during a single week (Table 1).

The SL of larvae reaching the estuary (Table 2) follows a similar pattern to age. Except in one instance (3 February), the first two and the last five cohorts to reach the estuary had a mean SL <13.9 mm. In the middle period, the weekly mean SL of larvae was generally larger. The difference between the smallest and largest mean SL of larvae of any one birthweek cohort throughout the recruitment period varied from 0.3 to 11.7 mm. This was generally related to the total time during which a cohort recruited to the estuary.

Abundance of birthweek cohorts Several birthweek cohorts contributed substantially to more than one of the recruitment peaks. Three cohorts (13, 20, 27 December) contributed at least 50% of their respective total recruits to the large influx of larvae that occurred on 23 March (Table 1). The high densities of larvae (Fig. 2, Table 1) captured on 10 and 24 February, 23 March, and 13 April were collections to which some birthweek cohorts contributed ≥50% of their total recruitment (e.g., 1 and 8 November cohorts to catch of 13 April).

Oceanic abundance and age/size distribution of larvae

Abundance of larvae The highest densities of spot larvae collected offshore during January and February generally occurred in waters ≥30 m (Fig. 6). Densities there ranged from 24 to 68 larvae/100 m^3, but diminished toward the coast and further offshore toward the shelf break. In areas within 40 km of the coast at depths <30 m, densities were <5 larvae/100 m^3. Except for two larvae collected off Beaufort Inlet in January (Fig. 6A), no larvae were collected within 10 km of the coast. Larval densities in the estuary at Pivers Island were always higher than at any oceanic station <30 m deep within 40 km of the coast.

Spot larvae were collected at two of seven stations sampled east and north of Onslow Bay during January (Fig. 6A). In February, spot larvae were collected at all but one of these stations (Fig. 6B). Densities were relatively low except at the station nearest Onslow Bay.

Age and length distribution of larvae Ages of 351 spot larvae caught during oceanic sampling ranged from 9 to 69 d. Youngest larvae occurred farthest offshore, over the outer continental shelf and within the Gulf Stream (Fig. 7A,B). Age of larvae varied inversely with distance from shore along the Beaufort Inlet transect in January and February and the Oregon Inlet transect in February (Table 3, Fig. 7A,B). The mean age of larvae in Onslow Bay during February seems to increase toward shore from a dispersion center on the outer continental shelf south of Beaufort Inlet. Older larvae radiate to the north and west in Onslow Bay (Fig. 7B). Larvae in the transect across the continental shelf off Oregon Inlet (Fig. 7B) may have a general spawning area in common with larvae collected in Onslow Bay.

The length of larvae also varied inversely with distance from shore (Table 3, Fig. 7C,D). Smallest larvae were found on the outer continental shelf and over the continental shelf break. The mean size of larvae was 3.4 mmSL (range 2.1–10.1 mm) in January and 6.2 mmSL (range 2.5–12.7 mm) in February.

Spawning time Spot larvae collected off North Carolina were spawned over the period 8 November to 17 January (Fig. 8). As many as six cohorts were found in any one sample and the overall mean number of cohorts per sample was three. In 19 of 33 stations, ≥50% of the larvae were from one cohort, and in six stations ≥50% were from two consecutive cohorts. The remain-

Table 1

Relative abundance of back-calculated birthweek cohorts of larval spot *Leiostomus xanthurus* (larvae/100 m^3) recruited to the Newport River estuary, 2 December 1987 to 4 May 1988.

	Birthweek cohorts (week beginning)																					
	October		November					December				January					February				March		
Capture date	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	31	7	14	21	28	6	13	Total
Dec. 2	0.48	0.24																					0.72
9	0.07																						0.07
17		0.64	0.96																				1.60
22			0.33	0.08																			0.41
30				9.81	2.45																		12.26
Jan. 6					5.29	2.64																	7.93
12					14.64	8.79																	23.43
20					4.45	4.45	13.34	13.34															35.58
27						26.69	8.90	8.90															44.49
Feb. 3		0.78	1.56	2.34	2.34	5.46	3.90	2.34		0.78													19.50
10			25.72	41.16	51.45	46.30	5.14																169.77
17					9.99	16.65	26.64	16.65	3.33	3.33													76.59
24					12.97	45.37	116.67	51.85	12.97														239.83
Mar. 3						1.50	5.23	8.22	0.75	0.75	0.75												17.20
9								6.50	6.50	9.74	9.74		3.25										35.73
16								6.32	7.90	11.06	3.16	6.32											34.76
23								50.66	33.75	135.07	151.92	84.41	50.66	16.90									523.37
30										5.03	20.10	15.08		5.03									45.24
Apr. 6											10.95	25.59	14.63										51.17
13												54.05	81.08	27.03	27.03								189.19
20															2.12	0.71		3.53	1.41				7.77
27																		0.16	0.16	0.47	0.16	0.16	1.11
May 4															0.14				0.55	0.82	0.55	0.14	2.20
% of total	0.03	0.11	1.85	3.47	6.72	10.25	11.67	10.70	4.23	10.76	12.76	12.04	9.71	3.18	1.90	0.05	0.0	0.24	0.14	0.08	0.05	0.02	

Table 2

Weekly mean standard length (mm) of back-calculated birthweek cohorts of larval spot *Leiostomus xanthurus* recruited to the Newport River estuary, 2 December 1987 to 4 May 1988.

	Birthweek cohorts (week beginning)																					
	October		November					December				January					February				March	
Capture date	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	31	7	14	21	28	6	13
Dec. 2	10.3	9.2																				
9	10.7																					
17		10.8	10.7																			
22			11.3	10.0																		
30				11.6	11.3																	
Jan. 6					11.9	9.3																
12					13.4	12.5																
20					15.3	14.7	13.3	11.9														
27						13.8	13.0	10.0														
Feb. 3		17.3	16.7	17.1	16.6	15.0	14.1	11.5		9.6												
10			19.2	18.2	17.9	17.3	17.4															
17					16.6	16.8	17.3	15.8	13.2	13.6												
24					17.4	16.8	16.9	15.4	14.0													
Mar. 3						20.0	20.1	18.5	14.9	13.8	12.9											
9								19.6	17.3	17.6	16.3		13.7									
16								20.1	19.5	18.4	17.4	16.8										
23								21.2	20.6	19.2	18.2	17.0	17.0	15.3								
30										19.1	18.9	18.5		17.6								
Apr. 6											18.8	18.3	17.4									
13												16.2	16.4	17.8	17.7							
20															17.1	16.3		13.3	13.4			
27																		13.0	12.3	12.3	12.6	10.8
May 4															16.2				13.8	13.2	13.4	11.2

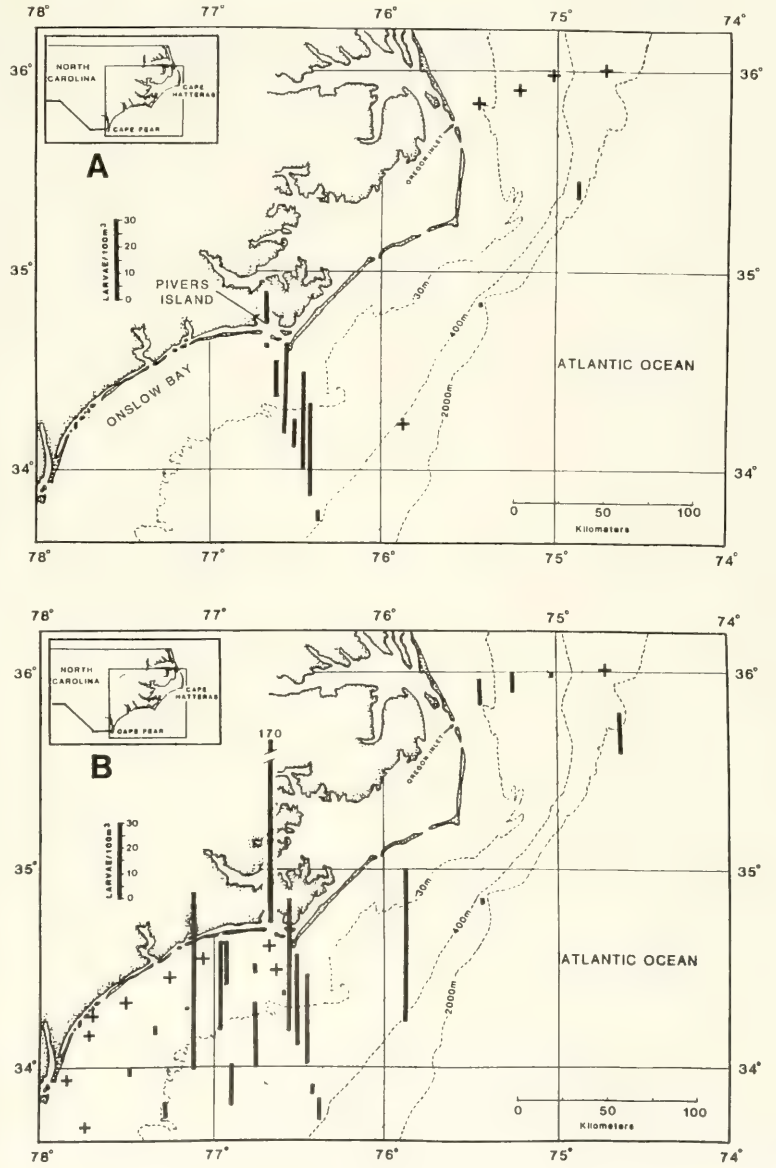

Figure 6

Density (larvae/100 m^3) of spot *Leiostomus xanthurus* larvae collected in 1988 with bongo nets off the North Carolina coast during **(A)** 12–13 January, and **(B)** 2–5 February, and at Pivers Island with a neuston net. + indicates no larvae collected.

ing eight stations each had <5 larvae. There were eight different birthweek cohorts in January and nine in February. The principal cohorts in January were those of weeks beginning 20 and 27 December, which together contributed more than 88% of all larvae collected in the ocean (Fig. 8). These cohorts were the most important contributors to larvae recruited during the week of greatest abundance, 23 March (Table 1, Fig. 2). During February, larval cohorts were principally from birthweeks beginning 20 December–23 January. Larvae from these cohorts were caught later in the estuary and contributed heavily to the abundance peaks of 23 March and 13 April (Table 1).

A Kolmogorov-Smirnov two-sample test (Sokal & Rohlf 1981) was used to compare larval birthdate distributions for a 3-week spawning period, 13 December–2 January (Figs. 5&8), for larvae collected during January–February in the ocean and February–March in the estuary. There was no significant difference (max. diff. = 0.108, $P>0.05$) between birthdate distributions of 98 larvae collected in the ocean in January and 109 collected in February. There was also no significant difference between the pooled birthdate distribution data for larvae collected in the ocean in January and February (n=207) and for 134 larvae collected in the estuary at Pivers Island (max. diff. = 0.180, $P>0.05$).

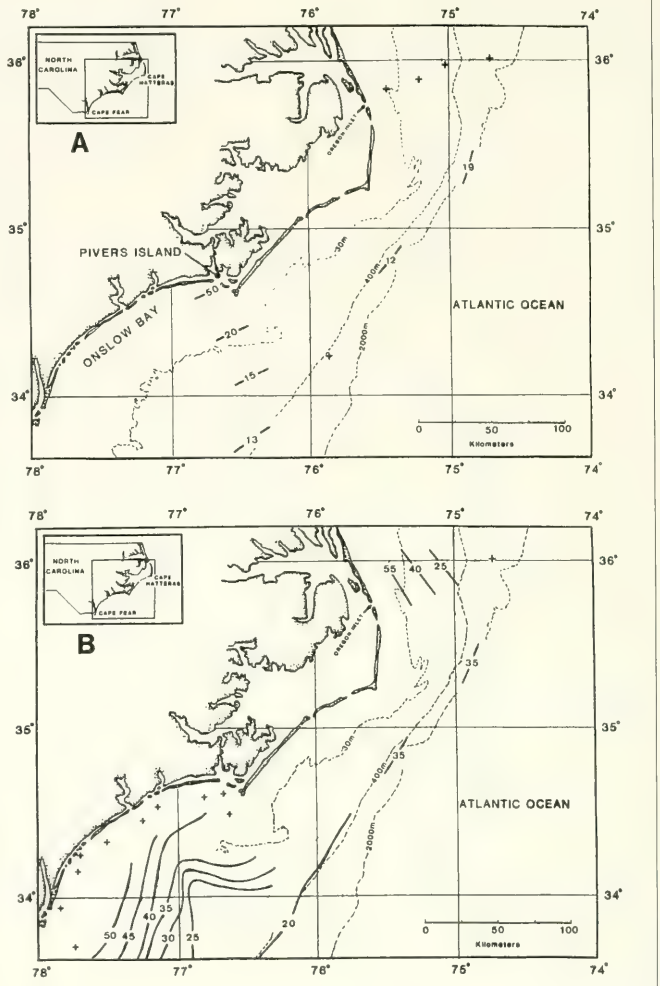

Figure 7

Contour plots of the mean age (d) on **(A)** 12–13 January, and **(B)** 2–5 February, and mean standard length (mm) on **(C)** 12–13 January and **(D)** 2–5 February, of spot *Leiostomus xanthurus* larvae collected off the North Carolina coast in 1988. + indicates no larvae collected.

Growth rate

The overall growth rate of larval spot was estimated from 312 estuarine and 351 oceanic specimens combined. Larvae ranged from 9 to 108 d and 2.1 to 22.2 mmSL (Fig. 9). From the Laird-Gompertz model (Fig. 9), we predicted that spot grew from 1.2 mm at hatching to 19.1 mm in 95 d, an overall average growth rate of 0.188 mm/d. The size at hatching, estimated from the Laird-Gompertz model (1.2 mmSL), was less

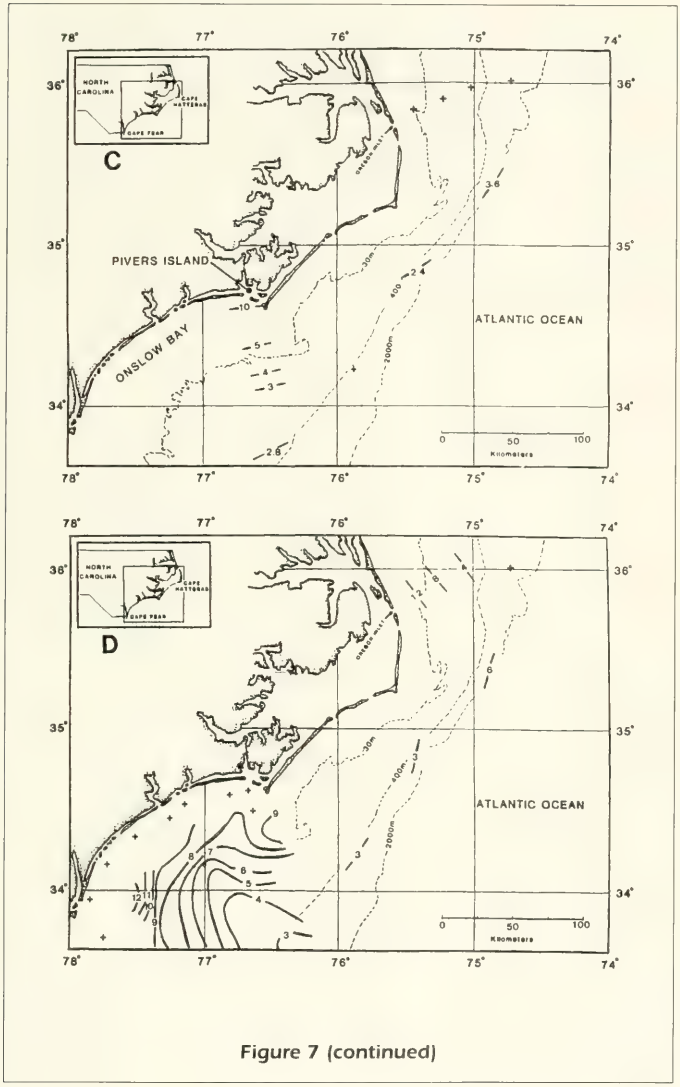

Figure 7 (continued)

than the 1.6–1.7 mmSL measured on laboratory-reared larvae by Powell & Gordy (1980) and estimated from wild specimens by Warlen & Chester (1985). In the log-transformed model (Fig. 9), age accounted for 98% of the variation in length. Age-specific growth rate declined from 5.8%/d at age 10 d to <0.7%/d at age 100 d. Maximum absolute growth rate occurred when larvae were 9.3 mmSL and 46 d old.

Within-season growth was compared for similar-age larvae collected at Pivers Island between early (early February) and late (early April) portions of the peak recruitment period and between early (early February) and post-peak recruitment periods (late April). The mean growth rate (0.195 mm/d) of 15 larvae (17.7±1.30 mmSL, 82.5±2.56 growth increments) collected 3 and 10 February (early peak) was not significantly different (t-test, P=0.09) from that (0.204 mm/d) of 15 larvae (18.2±0.98 mmSL, 81.9±3.19 growth increments) collected 6 and 13 April (late peak). However, the mean growth (0.214 mm/d) of 12 larvae (14.9±1.45mmSL, 62.3±3.77 growth increments) collected on 3 February (early peak) was significantly different (t-test, P<0.01) from that (0.194 mm/d) for 10 larvae (13.4±0.64 mmSL, 60.7±3.43 growth increments) collected in late April (post-peak).

Discussion

The spawning period of spot in the 1987–88 season was apparently a continuous process occurring over 5 months from mid-October to mid-March. Although spawning was protracted, the greatest concentration occurred in the 2-month interval from mid-November to mid-January when 90% of the estuarine-recruited larvae were spawned. This information, while generally agreeing with earlier work on fish collected in North Carolina (Hildebrand & Cable 1930, Warlen & Chester 1985) and South Carolina (Beckman & Dean 1984), is the first to be estimated from back-calculated birthweek distributions on larvae collected weekly over the entire estuarine recruitment period. The contribution of birthweeks to the larval catch each week was based on

Table 3

Linear regressions of mean estimated age (d) and mean standard length (mmSL) of spot *Leiostomus xanthurus* larvae on collection distance (km) from shore.

Transect/ month	Stations along transect	Variable	Intercept	Slope	Correlation Coefficient
Beaufort Inlet January	8	Age	44.875	–0.364	0.905
		SL	10.227	–0.088	0.886
Beaufort Inlet February	7	Age	68.345	–0.515	0.936
		SL	13.465	–0.104	0.953
Oregon Inlet February	3	Age	71.279	–1.526	0.999
		SL	15.756	–0.363	0.997

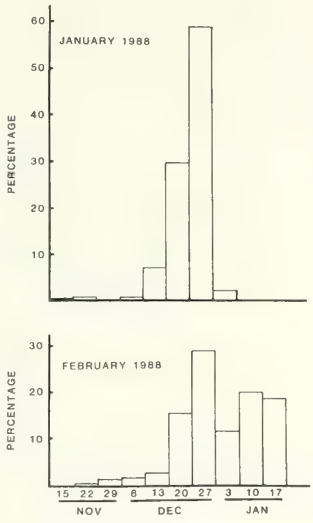

Figure 8

Percentage distribution of back-calculated birthweeks for spot *Leiostomus xanthurus* larvae caught in 1988 off the North Carolina coast: **(top)** 12–13 January and **(bottom)** 2–5 February.

the percentage age composition and density of larvae.

The seasonal differences in age and size of larvae at estuarine recruitment (Fig. 3) suggest that spawning may have been nearer the coast at the beginning and end of the spawning season. As adult spot emigrate from the estuary to offshore waters in fall, at a time of decreasing photoperiod and water temperature (Mercer 1989), they probably seek suitable water temperatures for spawning (17.5–25°C) (Hettler & Powell 1981). This temperature range is present over much of the North Carolina continental shelf water (Stefánsson et al. 1971) in the early months of spawning. During later spawning (mid-December to February), nearshore waters are cooler and well mixed and water above 17.5°C is generally restricted to areas on the outer continental shelf (Stefánsson et al. 1971, Atkinson 1985). Also, in winter the extent of this potential spawning area may be influenced by the Gulf Stream and its occasional wave-like perturbations (cyclonic meanders and filaments) along its western edge which can intrude onto the continental shelf. It is known that average surface-water temperatures on the outer continental shelf are moderated by the Gulf Stream (Atkinson 1985). The winter (January and February) distribution patterns of age and size of spot larvae in Onslow Bay, with the youngest, smallest larvae occurring only furthest offshore, support the idea that spawning may occur some 90 km offshore. Spawning that occurs further offshore as the spawning season progresses has been suggested for spot (Lewis & Judy 1983, Warlen & Chester 1985) and Atlantic croaker *Micropogonias undulatus* (Warlen 1982). Norcross & Austin (1988) also suggested that the area of warm water encountered upon migration of Atlantic croaker from Chesapeake Bay onto the continental shelf determines spawning location.

Differences in age at estuarine recruitment may also be due to differences in transport rate that result from the degree to which favorable currents facilitate more rapid transport of larvae toward shore. Different transport rates and spawning distances from shore could also act in concert to produce the observed differences in age and size at recruitment. Although some of the physical processes that could affect larval transport have been discussed (Checkley et al. 1988, Miller 1988, Pietrafesa & Janowitz 1988), precise larval-fish transport mechanisms still remain unknown.

The higher abundance of spot larvae in water deeper than 30 m may be a function of spawning location and subsequent larval transport toward shore. The reduced abundance observed inshore of the 30 m isobath may reflect fewer numbers of larvae present or their reduced vulnerability to capture by bongo nets. Mortality will also reduce larval abundance over time. Kjelson et al. (1976) and Miller et al. (1984) suggest that spot larvae offshore are more pelagic but that inshore they are more benthic-oriented. Spot larvae caught from shore to the 30 m isobath were 40–61 d old and 8.2–12.1 mm SL, and correspond to the early stages of the transformation period (Govoni 1980 and 1987, Powell & Gordy 1980) when spot begin to be more benthic.

Larval spot are recruited from offshore spawning areas to estuaries bordering Onslow Bay. Fish of the same ages also are found along the offshore to onshore Oregon Inlet transect (Figs. 6,7). This data and the fact that larval spot were found in and near the Gulf

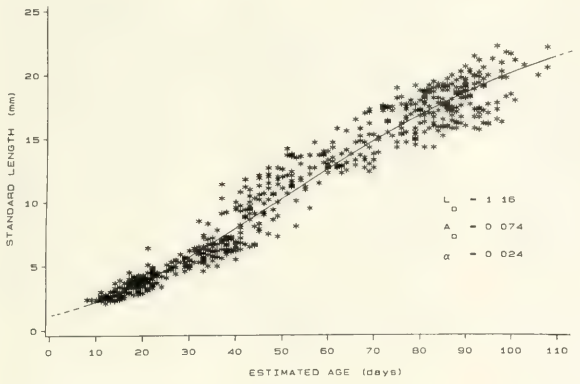

Figure 9

Growth of larval spot *Leiostomus xanthurus* collected from the estuary and oceanic waters off North Carolina, November 1987 to May 1988. A Laird-Gompertz model was fit to the age/size data for 663 fish. Estimates of the parameters were obtained by fitting the log-transformed version of the model to the data. L_0=length at hatching, A_0=specific growth rate at hatching, and α=exponential decay of the specific growth rate.

Stream (Fig. 6) suggest that larvae are being transported to areas north of Onslow Bay. The origin of these larvae is probably south of Cape Hatteras and most likely Onslow Bay or southward. These data support the hypothesis of Norcross and Bodolus (1991) that spot spawned south of Cape Hatteras on the outer continental shelf contribute to recruitment in Chesapeake Bay. Spring (March–May) spawned bluefish *Pomatomus saltatrix* are also thought to be transported to the Middle Atlantic Bight from spawning areas near the edge of a northerly flowing warm-water mass (Gulf Stream) in the South Atlantic Bight (McBride & Conover 1991).

The extended recruitment period of 5 months (Fig. 2) is a reflection of the length of spawning period (Fig. 5), although the time from spawning to recruitment varies throughout the season. The beginning of the maximum recruitment period coincides with increasing estuarine water temperature. Warlen & Burke (1990) found that peak immigration into North Carolina estuaries of fall–winter spawned ichthyoplankton matched the period of rising water temperature. This idea agrees with the fact that spot abundances are low during cold periods. Low water temperatures (<10°C) can cause cold stress by increasing larval respiration rate and can kill spot larvae (Hoss et al. 1988). The maximum estuarine recruitment period in North Carolina probably varys slightly from year to year, but is basically midwinter to early spring. Our estimate of the maximum recruitment period (mid-February to mid-April) is similar to that (February–March) recorded by Hettler & Chester (1990) and that (mid-January to mid-March) found by Warlen & Burke (1990). Apparently once spot larvae are in the estuary they move toward fresher water and utilize upper reaches of estuaries as nursery areas (Weinstein et al. 1980, Allen & Barker 1990). Peak recruitment of spot to the marshes of the Cape Fear River estuary in North Carolina occurred during March and April (Weinstein 1979). Interannual variations may be expected as a consequence of the seasonal changes that trigger emigration of the adults from estuaries to oceanic spawning areas and the subsequent transport rates of larvae back to the estuary.

The sum of the weekly mean larval densities over all collections (1540 larvae/100 m^3) was almost double that of 1985–86 (estimated from Fig. 2 of Warlen & Burke 1990), but less than that of 1989–90 and about equal to 1986–87 and 1988–89 (S.M. Warlen, unpubl. data). Allen & Barker (1990) also recorded variable patterns of larval spot abundance in South Carolina estuaries during 1981–84. The four highest peaks of recruitment density (10 and 24 February, 23 March, 13 April), that contributed about 74% of all spot larvae, could be consequences of concentration mechanisms of larvae outside the inlet and the subsequent facilitation of the influx of pooled larvae to the estuary. Lyczkowski-Shultz et al. (1990) suggested that larvae of spot, as well as other offshore spawners, accumulate in nearshore areas to develop and grow prior to recruitment. Tide may be an important mechanism which forces the larval gathering process outside and inside inlets (Pietrafesa & Janowitz 1988). The higher abundance of larvae just inside the inlet compared with the abundance at inshore stations seems to be a common feature for many estuarine-dependent species (Warlen 1982, Lewis & Judy 1983, Warlen & Chester 1985).

Because any birthweek cohort can be widely dispersed in the ocean, their larvae may reach the estuary over a period of 2–10 weeks. However, in general, >50% of the larvae of any birthweek cohort are recruited to the estuary in one week (Table 1). Birthweek cohorts of 25 October to 15 November had bimodal

recruitment, with small groups of younger larvae of each cohort reaching the estuary earlier, and larger groups of older (and larger) larvae recruited later (Tables 1, 2). The groups are clearly separated by a period of no recruitment, and the separation becomes less evident with later birthweek cohorts. The existence of two groups of recruits from early cohorts could result from dispersion of larvae spawned over the mid-continental shelf at different spawning locations and with different rates of transport to the estuary. Birthweek cohorts after November do not appear to be recruited to the estuary as distinct early and late groups.

The results show that the abundant larval cohorts of birthweeks 20 and 27 December, caught in January and February in Onslow Bay, contributed substantially to recruitment over the last four weeks in March. Birthweek cohorts of 3, 10, and 17 January were well represented in two later estuarine recruitment peaks. The comparison of birthdate distributions of larvae collected in the ocean in January and February and later in the estuary in February and March provided an opportunity to assess the relative survival of cohorts. The Kolmogorov-Smirnov tests showed no significant difference between ocean and estuarine birthdate distributions for larvae spawned over a period (13 December–2 January) of intense spawning. Therefore, we conclude that earlier (oceanic) and later (estuarine) larvae were from the same birthdate distribution, and that survival for the daily cohorts between 13 December and 2 January was not age-specific. The lack of seasonal sampling of larvae in the ocean precluded similar comparisons of birthdates throughout the spawning season.

During their oceanic existence, spot larvae grew rapidly from a hatching size of about 1.6 mmSL to a mean size of 17.2 mmSL at estuarine immigration. The growth curve was sigmoidal and similar to those found by Warlen & Chester (1985) for spot larvae in North Carolina during 1978–79 and 1979–80. Parameter estimates of the growth model for larval spot in 1987–88 in North Carolina, i.e., length at hatching ($L_{(0)}$=1.156), specific growth rate at hatching ($A_{(0)}$=0.074), and the exponential decline of the specific growth rate ($\propto$=0.024), were comparable to the growth parameter estimates for 1978–79 and 1979–80 ($L_{(0)}$=1.686, 1.609; $A_{(0)}$=0.060, 0.067; $\propto$=0.021, 0.026) found by Warlen & Chester (1985). Maximum growth rate (9.3 mm, 46 d-old larvae) was between the values that they report (8.0 mm, 46 d old; and 10.7 mm, 45 d old). There did not appear to be large differences in within-season growth of spot, although significant differences could be demonstrated. Mean growth was about 0.19–0.21 mm/d for larvae collected during and after the peak immigration period.

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Abstract—Spontaneous behavior of young red drum *Sciaenops ocellatus* was examined over a period of 8 h at two acclimation temperatures (21° and 26° C) and after acute temperature changes between these levels. Three sizes of fish were used ($\bar{x}$=9, 23, and 34 mmTL). Activity of fish acclimated to 26° C was greater than that at 21° C for fish of all sizes. Duration of pauses in spontaneous activity was generally lower at the warmer temperature. Effects of handling stabilized after 2–5 h. The time course for activity after an acute thermal change followed the traditional model for thermal stress, with an early overshoot followed by a stabilized period. The overshoot was positive for upward transfers (21–26° C) and negative for downward transfers (26–21° C). Pause duration showed a time course roughly inverse of the trend for activity, but pause frequency was inconsistent. Effects of 5° C changes stabilized after about 2 h. Results indicate that a minimum adjustment period of 2–5 h is advisable when handling young red drum for research or for stocking into natural waters. The behavior of young red drum deprived of food at acclimation temperatures suggests they are sweep, rather than saltatory, searchers.

Temperature effects on spontaneous behavior of larval and juvenile red drum *Sciaenops ocellatus*, and implications for foraging*

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Searching for food is critical to survival, and any factor that influences foraging behavior may have vital consequences, especially early in life when starvation is a serious threat. Temperature is one of the most potent natural factors affecting fishes, and substantial thermal variability may be experienced routinely. Such variability can span a wide range of time scales. Annual and seasonal differences in water temperature are common. Measurements of thermal effects on this scale probably reflect differences between physiologically stable (acclimated) states with respect to temperature. Differences in swimming performance due to acclimation temperature are well documented (Beamish 1978). Shorter-term temperature variations are also common in nature (summarized by Montgomery & MacDonald 1990). Fishes residing in shallow, lentic waters can experience large amplitude, diel temperature cycles (Bamforth 1962, Smid & Priban 1978). Movement across a thermocline imposes an even more rapid temperature change, as does inundation of tidal marshes and pools and the act of stocking hatchery fish into surface waters. Under these circumstances, the dynamic processes of physiological adaptation to the temperature change also contribute to the overall thermal effect.

Our goal was to examine the effects of temperature on spontaneous behavior of young red drum *Sciaenops ocellatus*. Here, we construe spontaneous behavior of solitary young fishes deprived of food as that typically used in foraging. We designed experiments to evaluate differences in behavior at two constant temperatures and after acute increase or decrease in temperature. Our measures of behavior are useful for quantifying foraging effort.

Materials and methods

All fish were reared from eggs spawned at the Fisheries and Mariculture Laboratory of the University of Texas Marine Science Institute. Spawning occurred in the evening at 27–28° C. Eggs were collected the following morning and placed in 150 L rearing tanks maintained at two nominal acclimation temperatures (21° and 26° C), where they hatched within 24 h of spawning. Larvae were fed rotifers (*Brachionus*) at 3–4 d after hatching (3 mmTL); *Artemia* nauplii were added to the diet at 10–11 d after hatching. Roti-

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fers were discontinued by day 15, when larvae were approximately 4–6 mm long. Dry food supplements were provided for larger fish, and *Artemia* densities were diminished so that juveniles eventually subsisted entirely on dry food. These and other details of rearing followed Holt et al. (1990).

Experimental design and protocol

Three sizes of red drum were studied. Mean (±SD) total lengths for the small, medium, and large size-classes were 8.7 (±0.9), 22.8 (±2.3), and 34.0 (±2.6) mm. The lower acclimation temperature (21°C) is well below optimum for red drum larvae (Holt et al. 1981), so those reared at that temperature grew more slowly and exhibited higher mortality rates during the first week than did the 26°C fish. Trials were conducted at both nominal temperatures, yielding four treatments. Trials on fish placed in water of the same temperature as their rearing tank (acclimation temperature) are termed 'high' (26°C) or 'low' (21°C) controls. Trials at a temperature differing from the acclimation temperature are referred to as 'upward' (21° to 26°C) or 'downward' (26° to 21°C) transfers.

For each trial, fish were transferred individually from the rearing tank to separate transparent experimental arenas and left undisturbed for the duration of the observations. Arenas were rectangular from above, with sides in a ratio of 5:3. Arena sizes were scaled such that the longer dimension of the rectangular surface area was 6 to 8 times the average total length of the fish. Water depth was 4.6 to 7.5 times the greatest body depth of the fish (3.5 to 7.5 times depth with fins expanded). Small fish were pipetted individually, while larger fish were released from 100 mL beakers containing a single fish in 50 mL of water from the rearing tank.

Behavior was recorded on videotape through a camera mounted above the arenas. The recorder was activated from about 1 min prior to transfer until 20 min after transfer, then for 5-min periods at intervals increasing from 15 to 60 min. In all, behavior was quantified during 19 5-min observation periods beginning 5, 10, 15, 30, 45, 60, 75, 90, 105, 120, 135, 165, 195, 225, 255, 315, 375, 435, and 495 min after transfer. Each of the four treatments was applied to six fish.

Temperatures in rearing tanks were controlled by balancing air temperature with submersed aquarium heaters, and were slightly above nominal levels. Mean acclimation temperatures during the 10 d preceding each trial were 21.3–21.7°C and 26.1–26.5°C. Temperature in the experimental arenas was maintained by controlling room air temperature. This sufficed for trials with medium and large fish; however, arenas for small fish were placed in a larger water bath to stabilize their temperature. During the 8h trials, the arena temperatures were 20.7–21.5°C and 26.1–26.5°C. By design, control fish were to experience no temperature change, and upward and downward transfers were to experience ±5.0°C. Actual differences between rearing tank and trial temperatures were –0.8° to +0.2°C for controls, +4.5° to +5.0°C for upward transfers, and –4.7° to –5.7°C for downward transfers.

In quantifying behaviors relevant to foraging, we recognized the dichotomy of searching techniques in fishes that travel in search of food and locate prey visually. Some species actively search while swimming and are called 'sweep' searchers (Laing 1938, O'Brien et al. 1986). Others search during brief periods when swimming is interrupted (described by Janssen 1982, and termed 'saltatory' searchers by O'Brien et al. 1989). Both types of active, visual foraging have been suggested for young fishes. For example, larval Atlantic herring *Clupea harengus* are thought to be sweep searchers (Rosenthal 1969, Rosenthal & Hempel 1970), while larval white crappie *Pomoxis annularis* exhibit saltatory searching behavior (Browman & O'Brien 1992). Bell (1990) suggested that the saltatory style is more generally employed by teleosts.

We examined three measures of foraging behavior: activity, pause frequency, and mean pause duration. Activity, the total amount of time spent swimming during each 5-min period, is a measure of foraging effort for sweep searchers, since they search new territory while swimming. Saltatory searchers use periods of inactivity (pauses) for finding food. Therefore, the frequency of pauses and their duration per observation period are indices of the time spent scanning the environment.

A BASIC computer program (available from the senior author) was written to act as an event recorder. Data were obtained by replaying the video tapes at normal speed and making the appropriate keystroke each time the subject's behavior changed (swimming, pausing). The program recorded intervals between keystrokes from which all variables were calculated. All observations from every trial (19 time-periods × 6 replicates × 4 treatments × 3 sizes = 1368 5-min observation periods) were made by the junior author. When a selection of observation periods was reanalyzed, the differences in activity averaged 4.1% (extremes 0.1–9.2%) of the combined mean.

Data analysis

Since observations within each temperature treatment and size-class followed the same individuals over time, repeated-measures multivariate analysis of variance (MANOVA) was used to identify effects on spontaneous behavior due to fish size, temperature, and time

since transfer. Each behavioral measure (activity, pause frequency, pause duration) was considered the 'trials' factor in a separate analysis. Size-class and temperature treatment were grouping factors. Activity was restricted, by definition, to values between 0 and 300 s. Data were expressed as a percentage of the total time-period, and an angular (arcsine) transformation was applied to satisfy the statistical requirement of MANOVA for normality (Snedecor & Cochran 1967). Pause frequency and duration were not transformed.

Further analyses focused on three questions: (1) How does behavior differ at the two acclimation temperatures? (2) What is the immediate effect of a transfer of 5°C on behavior (relative to fish maintained at acclimation temperatures)? and (3) When does behavior stabilize after such a transfer? These questions were addressed by repeated-measures MANOVA on pairs of treatments within size-classes. Since temporal trends in variables were of greater interest than the mere presence of significant differences among the time-periods, we examined first (linear)- through fourth (quartic)-order polynomial trends over time with univariate F statistics (Wilkinson 1990), in addition to testing for significant differences due to temperature treatments within each time-period.

By design, fish transferred upward or downward experienced a temperature change, but control fish did not. However, behavior of all fish could be expected to vary with time, due to effects of handling, hunger, or circadian rhythms. Effects of handling should diminish with time since transfer, but hunger should increase over time and have a stronger influence on behavior of smaller fish. Therefore, behavior of fish in transfers was compared with that of control fish from the same acclimation temperature to answer questions (2) and (3). Specifically, upward transfers were compared with the low controls, and downward transfers with the high controls, to examine changes in behavior relative to acclimation levels. Figures 2, 4, and 6 depict the effects of thermal transfers as differences between means of six fish in the transfer and control treatments, but statistical tests were based on results for individual fish.

Results

Spontaneous behavior was composed of conspicuous periods of swimming activity interspersed with pauses, which were sometimes quite long. Behavior of medium and large fish was grossly similar, their transitions from active swimming to pausing were gradual, in part because of passive coasting. At the larger sizes, swimming involved forward movements generated by the caudal and pectoral fins and complex maneuvers using sculling motions of the pectoral fins alone. Movements of small fish were less fluid. Their small size and low velocities prevented them from appreciable coasting, so their motion stopped abruptly when propulsive strokes of the caudal region ceased.

Activity

The proportion of time in active swimming was high for all sizes, usually ≥65%. However, there were significant differences in activity among the three size-classes, among the four temperature treatments, and within individuals over the course of the experiments. When the four temperature treatments were examined separately, significant differences among size-classes were found only for downward transfers and high controls (Table 1).

Activity varied significantly with time during experiments within most temperature treatments for small and medium fish (Table 1). Large fish showed no significant changes in activity with time in any of the treatments because variability among individuals was greater than at smaller sizes. Differences in activity over time constituted temporal trends for small fish in all treatments and medium fish in downward transfers. These trends were usually linear, but several higher-order polynomials were significant for downward transfers (Table 1). In subsequent comparisons of the different temperature treatments, we examined each size-class separately because of the highly significant differences among sizes.

Controls Activity was generally greater at 26°C for all sizes of fish (Fig. 1). This difference was significant for small and medium fish, but the attained significance, P, for large fish was slightly beyond the criterion of α=0.05 (Table 1).

Mean activity followed a monotonic trend with time at both temperatures for all sizes (Fig. 1). Small fish were most active immediately after transfer, while medium fish were least active at that time. Activity levels generally became stable within approximately 4 h. Mean differences (±SD) between the two control levels after 4 h were 40.0 (±12.9), 49.1 (±26.6), and 45.7 (±41.5) s of swimming/5 min for small, medium, and large fish, respectively. Thus, there was remarkable similarity in the effect of acclimation temperature on mean activity, but variability increased steadily with size.

Significant differences between acclimation temperatures were common during the first 2 h of the trials, and rare thereafter (Fig. 1), suggesting that the effect of handling on activity and the rate of recovery were temperature-related. However, these effects of temperature were not consistent. Activity of small fish stabi-

Table 1

Significance levels (P) for F tests in repeated-measures MANOVA of activity in red drum *Sciaenops ocellatus*. Boldface values indicate effects significant at α=0.05. Superscripts indicate the presence and order of significant polynomial trends with time (1=linear, 2=quadratic, 3=cubic, 4=quartic).

		Size-class			
Treatment	Effect	All	Small	Medium	Large
All	Size	**<0.001**			
	Treatment	**0.001**			
	Time	**0.001**			
Upward transfer	Size	0.060			
	Time	0.477	**<0.001** [1]	**0.045**	0.263
Low control	Size	0.092			
	Time	**0.027**	0.211 [1]	**0.008**	0.310
Downward transfer	Size	**0.027**			
	Time	**<0.001**	**0.030** [2,3,4]	**<0.001** [1]	0.856
High control	Size	**0.037**			
	Time	0.061	**<0.001** [1]	0.168	0.193
High control vs. low control	Treatment		**<0.001**	**0.035**	0.058
	Time		**<0.001**	**0.001**	0.256
Upward transfer vs. low control	Treatment		**0.031**	0.536	0.554
	Time		**<0.001**	**<0.001**	0.807
Downward transfer vs. high control	Treatment		**0.016**	**0.043**	0.214
	Time		**0.001**	**<0.001**	0.974

lized sooner at low temperatures, but activity of medium fish stabilized later at low temperatures.

Transfers The general response to a 5°C change was an almost immediate shift in activity in the expected direction (upward transfers produced higher activity, downward transfers produced lower activity) to a level greater than the stabilized value attained after about 2.5 h (Fig. 2). In upward transfers, elevated activity persisted for 1–2 h, rising during the first 20–30 min from an implicit value of zero just prior to transfer. The response of fish to downward transfer was an almost immediate drop in activity to minimum values followed quickly by increasing activity (Fig. 2).

Activity of small fish after upward transfer was significantly different from that of low controls (Table 1). Differences were concentrated in the early part of the experiments, when transferred fish were more active than controls in six of the first seven time-periods (Fig. 2). Medium and large fish did not show overall differences between upward transfers and controls (Table 1), and there were few significant differences at individual time-periods.

Downward transfer also had a significant influence on activity in comparisons with high controls, but only for small and medium fish (Table 1). Transferred fish were less active than controls in the first six time-periods for small fish and in five of the first nine time-periods for medium fish (Fig. 2). Large fish did not show an overall difference between downward transfer and control treatments, and only a single difference for individual time-periods was statistically significant (Fig. 2).

Pause frequency

The number of pauses during the 5-min observation periods generally decreased as fish grew (Fig. 3). Small control fish (temperatures and times combined) paused an average of 24.6 (±11.5) times in 5 min; medium and large fish paused 10.8 (±6.9) and 9.5 (±7.3) times, respectively. All main effects (size-class, temperature

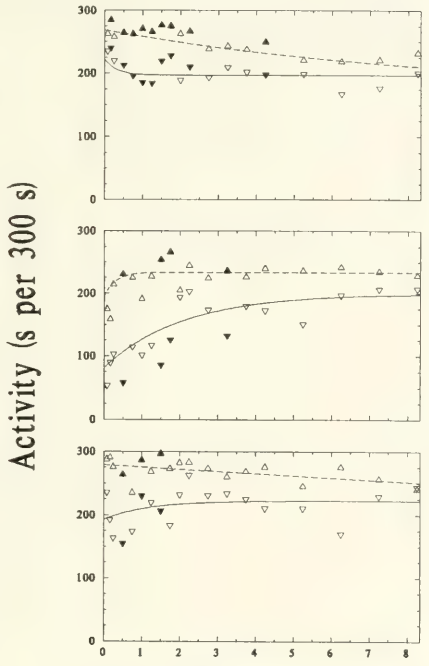

Figure 1

Time-course for activity of young red drum *Sciaenops ocellatus* at two acclimation temperatures. Points represent means of six observations. Upright triangles and broken lines refer to control trials at 26° C. Inverted triangles and solid lines refer to control trials at 21° C. Filled symbols denote periods in which activity differed significantly at the two temperatures. Panels show data for small (upper), medium (middle), and large (lower) fish.

treatment, and time since transfer) had a significant influence on pause frequency. Differences among the size-classes were present within each of the treatments (Table 2).

Within individual fish (all sizes combined) there were significant differences in pause frequency with time in all treatments except the downward transfers (Table 2). These differences among time-periods followed linear trends in most temperature treatments for small fish. Among medium and large fish, temporal trends were less common, but curvilinear (quadratic) relationships were significant in two combinations of temperature treatment and size-class (Table 2).

Controls Pause frequency differed significantly between the two control temperatures for small and large fish (Table 2). For those sizes, pause frequency was higher at 21° C (Fig. 3).

Pause frequency generally increased with time since transfer, but the amount of change during the experiment was small for medium and large fish. Temporal trends stabilized after about 2.5 h in most treatments (Fig. 3). Trends for small fish were parallel, with a mean difference of 13.6 (±4.1) additional pauses/5 min at 21° C. Large fish had roughly parallel trends during the first 3 h, with a mean difference over that period of 7.5 (±3.0) pauses. Mean differences between control values after behavior stabilized (3 h) were −12.9 (±2.0), 0.2 (±2.6), and −4.0 (±2.4) pauses/5 min for small, medium, and large fish, respectively.

Differences between the control temperatures during individual time-periods were present throughout the experiments on small fish. For the two larger sizes, significant differences were confined to the first 2.5 h, highlighting the converging trends for those sizes. It appears that an immediate effect of handling is to depress pause frequency. The magnitude and duration of the effect is temperature-dependent.

Transfers Small and large fish showed qualitatively similar responses to the 5° C temperature change, relative to control values. Pause frequency was depressed by upward transfer. For the same size-classes in downward transfers, pause frequency increased slightly at first, then dropped to values below controls (Fig. 4). The response of medium fish to upward transfer was similar in form to the downward transfer of the other size-classes. In downward transfers their response was the same as that of low controls, producing a corrected pause frequency of zero. Variability in these apparent differences was great, and the only significant difference between transferred fish and their controls was for small fish in upward transfers (Table 2).

Small fish paused consistently and significantly less often after experiencing a 5° C increase (Fig. 4, Table 2). Large fish showed a similar, though smaller and non-significant, response. Mean differences between upward transfers and low controls were −6.8 (±4.3) and −4.1 (±2.8)s for small and large fish, respectively. Differences at individual time-periods were rare in upward transfers, at all sizes, but the overall effect of time since transfer was always significant (Table 2).

Downward transfer did not result in a significant overall effect on pause frequency, relative to controls, for small, medium, or large fish (Table 2). However, there were temporal trends in the differences between

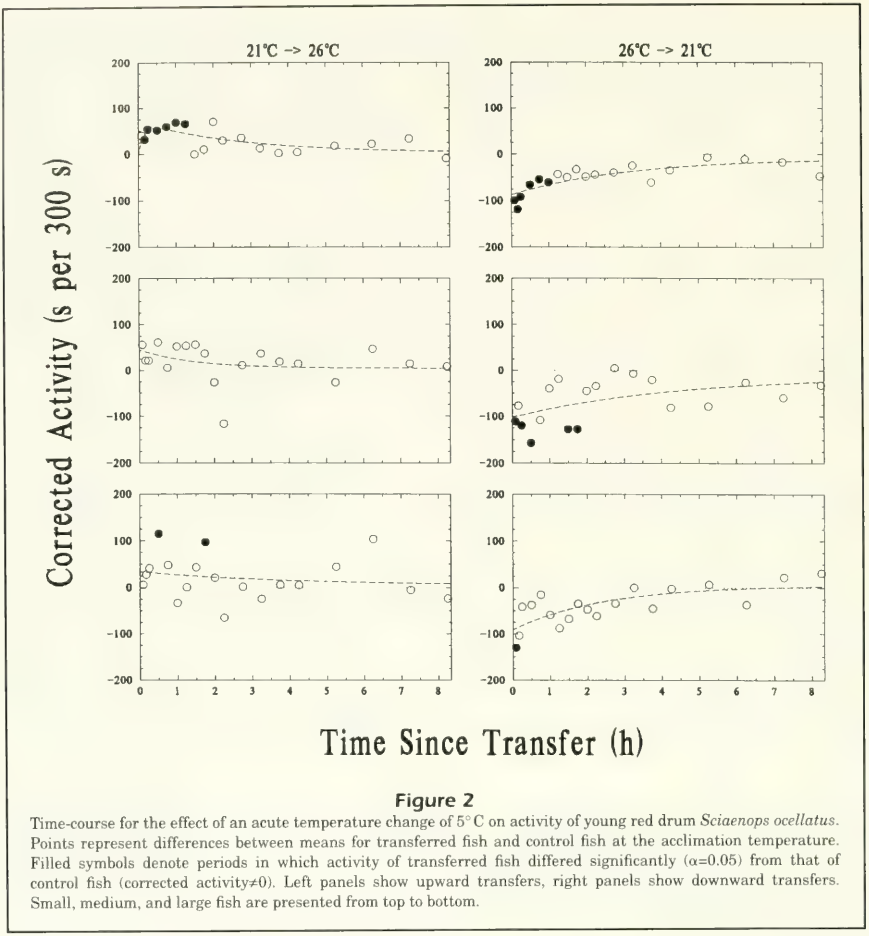

Figure 2

Time-course for the effect of an acute temperature change of 5° C on activity of young red drum *Sciaenops ocellatus*. Points represent differences between means for transferred fish and control fish at the acclimation temperature. Filled symbols denote periods in which activity of transferred fish differed significantly (α=0.05) from that of control fish (corrected activity≠0). Left panels show upward transfers, right panels show downward transfers. Small, medium, and large fish are presented from top to bottom.

downward transfers and high controls, centered near zero, that could not be detected by an overall test for a temperature effect. Corrected pause frequency of both small and large fish in downward transfers declined throughout the experiments, relative to high controls (Fig. 4). Time had a significant effect for these sizes but not for medium fish.

Pause duration

This variable showed the greatest range of variation, spanning more than two orders of magnitude (note varying scales in Figs. 5&6). Small fish showed little effect of time or temperature treatment on pause duration, relative to effects on larger fish. At the two larger sizes, pauses were longest at the start of the experiments, stabilizing after about 2.5 h. As with the other behavioral measures, all main effects were significant (Table 3).

There were significant differences in pause duration among time-periods for low controls and downward transfers (Table 3). Linear, quadratic, and cubic trends described temporal changes for small and medium fish, but no trends were found for large fish.

Controls Pause duration was generally greater for fish maintained at 21° C than for those held at 26° C (Fig. 5). Largest differences occurred early in the ex-

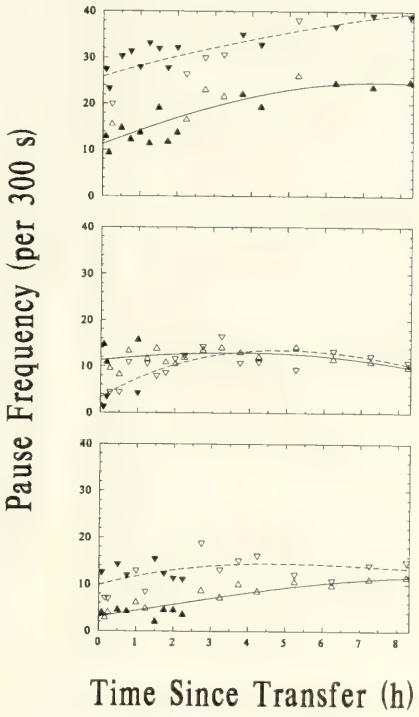

Figure 3
Time-course for pause frequency of young red drum *Sciaenops ocellatus* at two acclimation temperatures. Annotated as in Fig. 1.

periments and their magnitude varied greatly with fish size. Small fish showed the least difference between controls, with a maximum of 2.2 s. Mean values for medium fish controls differed by as much as 207.2 s during a given time-period (Fig. 5). Overall differences between the control temperatures were significant only for medium fish.

Pause duration was highest at the start of trials, with longer pauses at 21°C than at 26°C. Pause duration at the lower temperature decreased over time, approaching levels seen at 26°C, but remaining above them throughout the experiments (Fig. 5). This temporal trend was supported by a significant effect of time since transfer for medium fish, but a smaller change and greater variability precluded a significant comparison for large fish (Table 3). Small fish showed much more subtle effects of transfer, although there was a significant effect of time due to a rising trend at 26°C. Pause duration generally decreased with time, reaching stable values within 1.5 h (Fig. 5). Mean differences (high control minus low control) after 2 h for small, medium, and large fish were −0.2 (±0.7), −7.7 (±3.9), and −8.3 (±19.2) s, respectively.

Transfers Upward and downward transfers had little effect on pause duration after about 2 h. The initial effect of a 5°C change on pause duration was consistent across the size-classes, but its magnitude varied greatly. Generally, an increase in temperature produced initially shorter pauses than in low controls. Downward transfer had the opposite effect, relative to high controls; pause duration increased. The medium size-class was affected most strongly (Fig. 6). The shock of an acute temperature drop was apparently more serious than a comparable increase in temperature. All size-classes showed a statistically significant change in pause duration after a drop in temperature, while none of the size-classes were significantly affected by an increase (Table 3). In contrast, temporal differences in pause duration were more prominent in upward transfers, where small and medium fish were significantly affected. Only medium fish showed significant differences with time in downward transfers, despite numerous significant differences at individual time-periods for small fish (Fig. 6).

Discussion

Transient thermal effects

The most widely accepted model for the time-course of adaptation of physiological rates to temperature change contains three phases (Kinne 1963, Prosser 1964, Precht et al. 1973). An initial shock reaction occurs during the first seconds to minutes, in which the rate overshoots the level expected for the new temperature. Over a period of minutes to hours, the rate returns from these extreme values to a stabilized level. The final stage occupies a prolonged period over which the final acclimated level is reached, but this may require weeks or months. This paradigm allows for two general cases. After exposure to a higher temperature, the overshoot for most measures is positive; the rate increases. When the destination temperature is lower than the acclimation temperature, the overshoot is negative (sometimes called an undershoot); the rate drops below that of the stabilized and acclimated levels for the colder temperature.

Table 2

Significance levels (P) for F tests in repeated-measures MANOVA of pause frequency in red drum *Sciaenops ocellatus*. Boldface values indicate effects significant at α=0.05. Superscripts indicate the presence and order of significant polynomial trends with time (1=linear, 2=quadratic).

		Size-class			
Treatment	Effect	All	Small	Medium	Large
All	Size	**<0.001**			
	Treatment	**<0.001**			
	Time	**<0.001**			
Upward transfer	Size	**<0.001**			
	Time	**0.005**	**0.004** [1]	0.076 [2]	0.122
Low control	Size	**<0.001**			
	Time	**<0.001**	**0.023** [1]	**<0.001** [1]	0.120
Downward transfer	Size	**0.039**			
	Time	0.544	**0.010**	0.114	0.944
High control	Size	**0.001**			
	Time	**<0.001**	**0.001** [1]	0.778	**<0.001** [1,2]
High control vs. low control	Treatment		**<0.001**	0.281	**0.024**
	Time		**<0.001**	**0.003**	**0.001**
Upward transfer vs. low control	Treatment		**0.021**	0.815	0.076
	Time		**<0.001**	**<0.001**	**0.009**
Downward transfer vs. high control	Treatment		0.979	0.945	0.489
	Time		**<0.001**	0.529	**0.018**

Activity of young red drum closely followed the traditional time-course at all sizes, whether the transfer was upward or downward. The general temporal trends in activity had similar shapes and values within treatments. Similar experiments conducted on a single size ('underyearlings') of Atlantic salmon also showed that spontaneous activity followed the overshoot model for adaptation (Peterson & Anderson 1969). Interestingly, activity of salmon did not decrease dramatically in downward transfers, as predicted. Rather, the time-course for activity followed trends similar to those resulting from temperature increases. Peak activity in the overshoot period correlated with the rate of temperature change, rather than the magnitude or direction of the change. Also, peak activity for salmon transferred to 12° C from 6° C was considerably lower than that for fish undergoing a similar downward transfer from 18° C. Our data show a similar relationship between the direction of transfer and mean peak (positive or negative) activity during the overshoot period. Upward transfers resulted in lesser overshoots of activity than downward transfers, and overshoot periods were later and prolonged. The differences were not as great as those found by Peterson & Anderson (1969) for salmon, probably because of the smaller differences between acclimation temperatures in our experiments (5° vs. 12° C).

To our knowledge, no other investigators have examined the influence of acute temperature change on pause characteristics. Pause duration followed trends that were broadly similar to the overshoot model and consistent across sizes. Variability around the trends increased with size of fish. Unlike activity, peak pause duration was essentially independent of the direction of temperature change, but there were differences among sizes. Pause frequency showed fundamentally different time-courses. These were not consistently related to the direction of temperature change or fish size. Pause frequency obviously is not a good indicator of the state of thermal adaptation. Its lack of uniformity suggests that it is highly variable and may be influenced by numerous other factors.

Acclimation differences

Activity also exhibited the strongest and most consistent effects of different constant temperatures in young red drum. In control experiments, the pattern of activ-

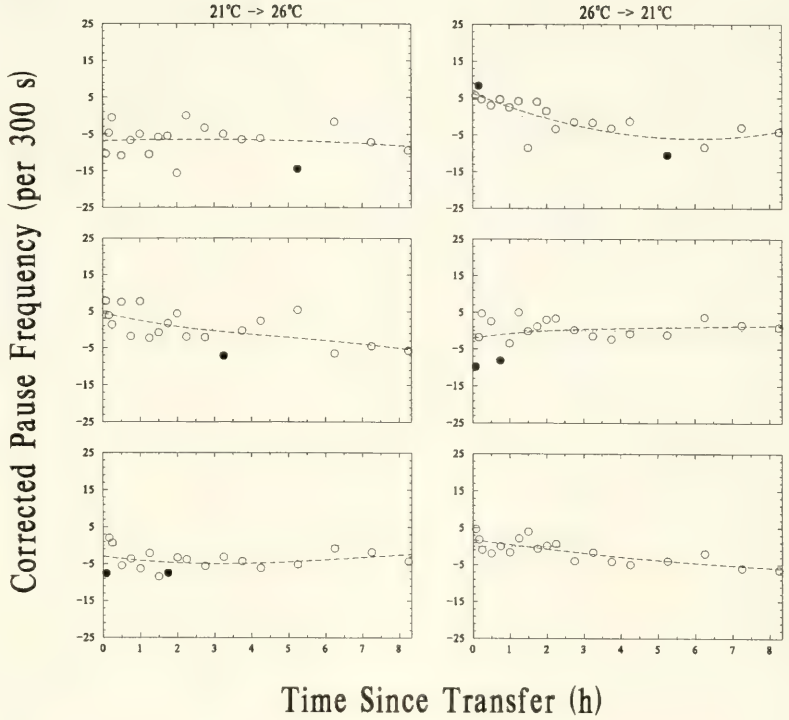

Figure 4

Time-course for the effect of an acute temperature change of 5° C on pause frequency of young red drum *Sciaenops ocellatus*. Annotated as in Fig. 2.

ity over time followed similar trends at the two temperatures within each size-class, showing the same initial response in activity followed by stable behavior after 2–4 h. Once stabilized, the proportion of time spent actively swimming was 21–26% greater at the higher temperature. This is equivalent to a temperature coefficient (Q_{10}) of 1.5–1.6, which is similar to values reported for various other whole-animal measures of fish swimming. Maximum sustainable speed of carp has a Q_{10} of 1.5–1.6 (Rome et al. 1984). Larval zebra danio and Atlantic herring have temperature coefficients between 1.4 and 1.7 for burst distance and maximum burst speed (Fuiman 1986, 1991). Larger rainbow trout have values of 1.8 for burst distance (Webb 1978).

Stabilized activity (after 4 h) in the control experiments, combined with pause frequency, describe a temperature effect on the duration of active bouts between pauses. The average duration of active bouts is very nearly the ratio of total activity to pause frequency, since pause frequency is essentially equal to the number of active periods. Higher values for activity at the upper temperature, accompanied by lower or equivalent pause frequencies, result in longer periods of activity in warmer water. This effect holds for all three size-classes, although the magnitude of the effect is greatest for small fish.

All variables we evaluated relate to foraging activity, and since fish were not fed during the experiments, there should have been ample motivation for fish to

Table 3

Significance levels (P) for F tests in repeated-measures MANOVA of pause duration in red drum *Scieanops ocellatus*. Boldface values indicate significant effects at α=0.05. Superscripts indicate the presence and order of significant polynomial trends with time (1=linear, 2=quadratic, 3=cubic).

		Size-class			
Treatment	Effect	All	Small	Medium	Large
All	Size	**<0.001**			
	Treatment	**0.014**			
	Time	**<0.001**			
Upward transfer	Size	**0.027**			
	Time	0.080	**<0.001** [1]	0.174	0.410
Low control	Size	**0.013**			
	Time	**<0.001**	0.071	**<0.001** [1,2,3]	0.420
Downward transfer	Size	**0.039**			
	Time	**0.022**	0.379 [2]	**0.024** [1]	0.729
High control	Size	0.183			
	Time	0.203	**0.001**	0.391	0.437
High control vs. low control	Treatment		0.062	**0.033**	0.202
	Time		**0.001**	**<0.001**	0.474
Upward transfer vs. low control	Treatment		0.134	0.224	0.500
	Time		**0.009**	**<0.001**	0.476
Downward transfer vs. high control	Treatment		**0.035**	**0.036**	**0.026**
	Time		0.310	**0.011**	0.781

search for food once the effects of handling subsided. Fish in warmer water would be expected to have a higher demand for food at any time in the experiment due to a higher metabolic rate. Further, small fish should have a higher demand than larger fish. Increased demand for food should be met by an increase in the volume searched per unit time.

The means by which a fish increases the volume searched per unit time depends on the type of searching employed (i.e., sweep vs. saltatory). Search volume for sweep searchers is proportional to the distance traveled. A sweep searcher in warmer water should swim faster, for longer periods, and/or pause less often. For saltatory searchers, search volume is directly proportional to pause frequency. Saltatory searchers can scan greater volumes by increasing both pause frequency and swimming speed between pauses. In the absence of suitable prey, their pause duration should be constant and only as long as necessary to scan each field completely. Our results for total activity and mean bout duration from the stabilized levels of control experiments follow the predictions for a sweep searcher: In warmer water, activity is higher, pause frequency is shorter, and the duration of active bouts is longer. Predictions for a saltatory searcher are contradicted, since pause frequency is not higher in warmer water. In fact, the opposite is true for small fish, which should be most strongly affected by hunger.

Conclusion

Experimental conditions cannot mimic the various natural scenarios of transient temperature fluctuation. Diel temperature changes are usually gradual and predictable. Yet, even when acclimated to regular circadian cycles, swimming behavior may be influenced by ambient temperature (Fuiman 1986). Traversing a thermocline is more abrupt, but it is predictable and at least partly voluntary, allowing for some degree of physiological preparation. Such vertical migrations can be beneficial to a fish's daily energy budget (Brett 1971, Wurtsbaugh & Neverman 1988), but there may

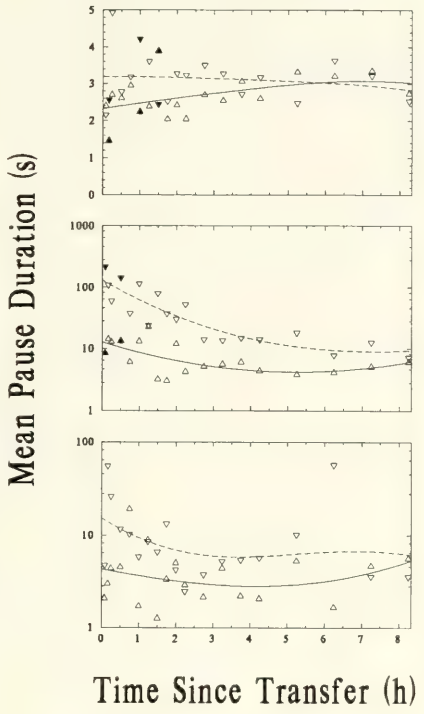

Figure 5
Time-course for pause duration of young red drum *Sciaenops ocellatus* at two acclimation temperatures. Annotated as in Fig. 1.

be an immediate cost in terms of locomotor efficiency. Perhaps the most hostile type of natural temperature fluctuation is exemplified by inundation of tidal pools. It is both unpredictable and abrupt, and concomitant physical changes (e.g., sound and pressure) probably add to the thermal effects on behavior. Our results show that acute temperature changes of 5° C alone engender behavioral changes that persist for about 2 h. These changes may act directly on a fish's ability to forage normally, or they may be merely indicators of a generally stressed condition in which a fish could be more susceptible to predators or disease.

In addition to the thermal impacts, our fish exhibited a handling effect which was overcome in 3–5 h. The most similar circumstance experienced by young red drum in the field occurs during stocking from hatcheries into natural waters. Young red drum, 3–40 mm in length, have been stocked into bays and estuaries routinely since 1975 (Dailey 1991). Stocked fish experience the combined effects of handling and temperature change (often more than 5° C). Similarly, fish used in laboratory experiments often incur handling and thermal stress. Our results suggest that even careful handling affects behavior for at least as long as a 5° C temperature change. Minimal handling and an acclimation period of 2–5 h would benefit young red drum during both laboratory experiments and stocking.

Acknowledgments

This research was supported by a grant from the Sid W. Richardson Foundation. We are grateful to Dr. Connie R. Arnold, Janie Muñoz, and Dana Allen for providing red drum eggs. Gerald R. Hoff and Dennis M. Higgs assisted in caring for the fish.

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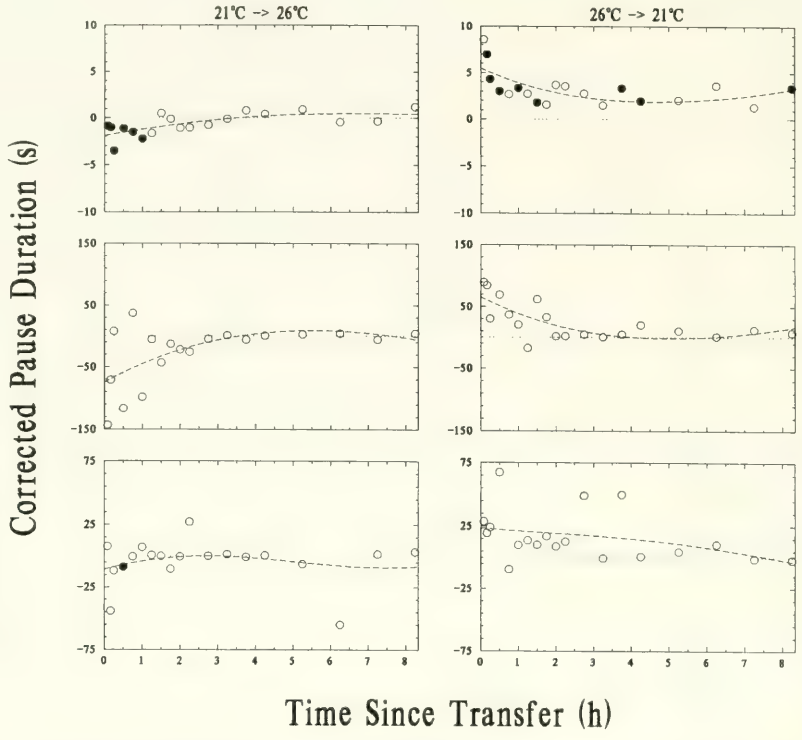

Figure 6

Time-course for the effect of an acute temperature change of 5°C on pause duration of young red drum *Sciaenops ocellatus*. Annotated as in Fig. 2.

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Abstract.—Ichthyoplankton were sampled weekly in Auke Bay, southeastern Alaska, from March or early April through June, 1986–89. The spring primary production bloom occurred in April, and was followed in May by the annual maximum in herbivorous copepods. Each year, the five most-abundant fish larvae were osmerids, Pacific sandlance *Ammodytes hexapterus*, walleye pollock *Theragra chalcogramma*, flathead sole *Hippoglossoides elassodon*, and rock sole *Pleuronectes bilineatus*. Each species tended to occur at the same time every year, and could be categorized either as synchronous species that were present at the time copepod abundance was maximized, or early species that were most abundant before the spring phytoplankton bloom. Pacific sandlance and rock sole larvae always reached maximum abundance prior to the spring bloom, whereas larvae of walleye pollock, flathead sole, and osmerids were most abundant at the time of the copepod maximum. Physical and biotic conditions experienced by early and synchronous larvae differ markedly, suggesting that survival through early life history is determined by different processes in the two groups.

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Abundance patterns of marine fish larvae during spring in a southeastern Alaskan bay

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Fluctuation in recruitment to exploited fish populations remains a central problem in marine fish management. There are indications that much of the variation in year-class abundance in marine fish populations results from processes and events in planktonic early-life-history stages (Houde 1987, Pepin & Myers 1991). Interannual variation in survival through egg and larval life stages is undoubtedly determined by multiple and interacting mechanisms; however, timing of reproduction has often been implicated as a factor contributing to the success or failure of year-classes. For example, Hjort's (1914) critical-period hypothesis and Cushing's (1975) match-mismatch hypothesis describe the importance of synchrony between production of larval fishes and their planktonic prey.

In subarctic regions, nearshore marine ecosystems display marked seasonal changes in physical and biotic conditions (Smetacek et al. 1984). In such systems, timing of reproduction may be extremely important, as conditions that result in high survival through planktonic life-history stages may be transitory. A dominant feature in the annual subarctic nearshore production cycle is the spring phytoplankton bloom, an event that contributes much of the annual production (Smetacek et al. 1984). The phytoplankton bloom is followed by the herbivorous copepod maximum (Smetecek et al. 1984), a period of 1–2 months that produces an annual optimum in foraging conditions for those larval fishes that feed on copepod nauplii. Water temperature and predator density may also determine survival of fish eggs and larvae (Houde 1987) and could constitute important constraints on timing of reproduction.

In this paper we report the results of a 4-year investigation of larval fishes in a coastal subarctic marine ecosystem. Our observations describe when larvae of some northeast Pacific Ocean fish species occur relative to the spring production cycle. The study was part of an interdisciplinary project (APPRISE, Association of Primary Production and Recruitment in a Subarctic Ecosystem) that provided a detailed description of the physical and biotic environment present during the period from late winter through early summer.

Study area

The study was conducted in Auke Bay (lat. 58° 22′ N, long. 134° 40′ W), southeast Alaska. (Fig. 1). The 16 km^2 Bay varies in depth from 40 to 60 m. Physical conditions in Auke Bay are typical of nearshore subarctic marine

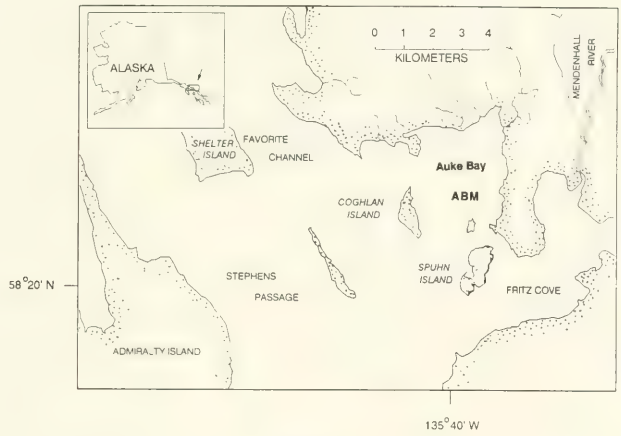

Figure 1

Auke Bay study area in southeast Alaska, and location of the Auke Bay Monitor (ABM) station.

Materials and methods

Fish larvae were collected in Auke Bay at a station designated ABM (Fig. 1) from mid-March or early April through mid-June, 1986–89. The ABM station was selected because it had been used in previous studies (summarized in Coyle & Shirley 1990). Samples were collected on the same day each week between 0800 and 1300, with the exception on the second week of April 1986 (Fig. 4). Each week five replicate samples were collected with a 1 m^2 Tucker trawl constructed of 505 μ mesh and fitted with a digital flowmeter in the middle of the net opening. Each replicate was collected at the ABM station by towing the net in a double-oblique trajectory to a depth of 30–35 m. The vessel

systems. The water column is isothermal until April, when surface warming and increased freshwater runoff contribute to formation of a pycnocline (Bruce et al. 1977, Ziemann et al. 1991). In the 4 years of this study water temperature prior to stratification varied from 3° to 5°C, was colder in 1986 and 1989, and warmer in 1988 (Fig. 2; data from Ziemann et al. 1990). Stratification, indicated by diverging temperatures at 5 and 20 m, began in April (Fig. 2; data from Ziemann et al. 1990).

Auke Bay exhibits a typical subarctic annual production cycle (Williamson 1978, Ziemann et al. 1991). The spring phytoplankton bloom began in early April, 1986–89 (Fig. 3; data from Ziemann et al. 1990), in response to several consecutive days of relatively high light levels (Ziemann et al. 1991). Chlorophyll biomass peaked in late April or early May each year, with a subsequent decline resulting from nutrient limitation (Ziemann et al. 1991). The herbivorous copepod maximum began 2–4 weeks after the spring phytoplankton bloom (Fig. 3; data from Coyle & Paul 1990), with *Pseudocalanus* spp. copepods dominant in every year (Coyle et al. 1990). Copepod nauplii in the size-ranges consumed by larval fishes were typically in low density prior to the herbivorous copepod maximum and reached maximum density in May, although there was considerable interannual variation in nauplii density during the period of peak abundance (Paul et al. 1991).

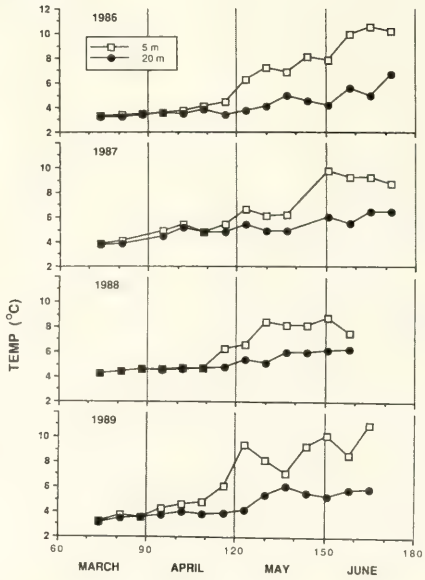

Figure 2

Spring and early-summer water temperatures in Auke Bay, Alaska, at 5 and 20 m (1986–89; data from Ziemann et al. 1990).

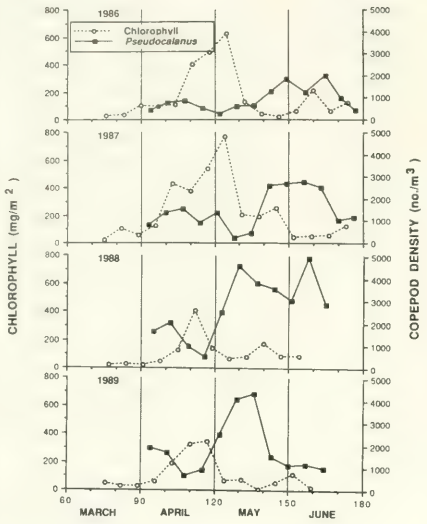

Figure 3

Chlorophyll concentrations and densities of *Pseudocalanus* spp. in Auke Bay during spring and early summer 1986–89 (chlorophyll data from Ziemann et al. 1990, *Pseudocalanus* data from Coyle & Paul 1990).

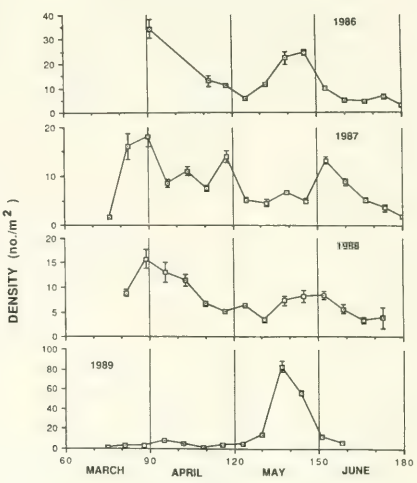

Figure 4

Mean densities of all fish larvae, excluding osmerids, in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

speed was about 1.5 kn. Each tow lasted 7–8 min, and volume filtered was typically around 300 m^3. Volume filtered per tow was very similar among years. Tows were collected on reciprocal compass courses set at 90° to the wind direction.

Fish larvae were removed from each replicate and enumerated by species, with the exception of osmerids, agonids, cottids, and cyclopterids, which were identified only to family. Osmerids were not identified to species because larvae of eulachon *Thaleichthys pacificus* and capelin *Mallotus villosus*, the two species common in the Auke Bay area, are very similar. The other three families (Agonidae, Cottidae, and Cyclopteridae) lack comprehensive identification guides to the species level. Mean densities of each taxon were calculated as the number/m^2 of surface.

Results

Total number of larvae collected annually ranged from 6087 in 1988 to 18,655 in 1986 (Table 1). Most of the interannual variation was due to differences in catches of osmerids. The five most-abundant taxa in all years were osmerids, Pacific sandlance *Ammodytes hexapterus*, walleye pollock *Theragra chalcogramma*, flathead sole *Hippoglossoides elassodon*, and rock sole *Pleuronectes bilineatus*. We did not include cottids in this summary, as they include at least eight species, none of which was exceptionally abundant; whereas the osmerids were very abundant, and included two species.

Total abundance of all larvae, excluding osmerids, peaked in March or early April of 1986–88 and in May 1989 (Fig. 4). Osmerids were excluded from total abundance estimates because in 1986 and 1987 their abundance obscured patterns associated with seasonal cycles of other species. In all years, osmerid abundance peaked from late May through June (Fig. 5). Such consistency in time of appearance in Auke Bay was typical of most species.

Larvae present in late March or early April were well in advance of either the spring phytoplankton bloom or the herbivorous copepod maximum. These early peaks in abundance were due primarily to high numbers of Pacific sandlance and rock sole (Figs. 6,

Table 1

Taxa of larval fishes collected in Auke Bay, Alaska in the spring, 1986–89, with total number collected (and rank order, in parentheses) of the five most frequently collected taxa in each year. The number of weekly samples, each consisting of five replicates, is indicated below each year.

	1986		1987		1988		1989	
	12		16		14		13	
Clupeidae								
Clupea harengus	67		125		128		283	
Osmeridae	11975	(1)	9704	(1)	336	(4)	1006	(3)
Ammodytidae								
Ammodytes hexapterus	1926	(2)	2829	(2)	2295	(1)	611	(4)
Bathylagidae								
Leuroglossus schmidti	121		401		155		326	
Gadidae								
Theragra chalcogramma	1696	(3)	856	(3)	1453	(2)	4618	(1)
Gadus macrocephalus	0		4		2		0	
Stichaeidae								
Anoplarchus insignis	221		108		103		114	
Lumpenella longirostris	108		63		110		210	
Lumpenus sagitta	175		178		75		150	
Ptilichthyidae								
Ptilichthys goodei	5		3		7		6	
Cryptacanthodidae	17		35		7		18	
Cottidae*	541		531		306		860	
Agonidae	396		404		216		334	
Cyclopteridae	26		34		14		31	
Pleuronectidae								
Hippoglossoides elassodon	474	(4)	428	(5)	303	(5)	2741	(2)
Pleuronectes bilineatus	409	(5)	522	(4)	406	(3)	449	(5)
Pleuronectes asper	146		104		1		5	
Pleuronectes vetulus	84		131		24		2	
Platichthys stellatus	171		142		85		427	
Psettichthys melanostictus	71		93		22		122	
Unidentified	26		33		41		47	
Total	18655		16724		6087		12360	

*Not ranked; included at least 8 species.

7). Two less abundant species—longsnout prickleback *Lumpenella longirostris* and slender cockscomb *Anoplarchus insignis*—also appeared early in 1987 and 1988, but had maximum density in May of 1989.

Two of the most abundant species, walleye pollock and flathead sole, consistently appeared in May (Figs. 8, 9) and were well synchronized with maximum density of copepods. Less common larvae that also tended to reach maximum density in May were starry flounder *Platichthys stellatus* and poachers (agonids) (Figs. 10, 11).

Discussion

It has been observed that many fish larvae occur in approximate synchrony with maximum zooplankton densities (Sherman et al. 1981 and 1984, Townsend 1984, Jenkins 1986). The strategy of synchronizing production of larvae to high abundance of prey has obvious adaptive value, and is the prerequisite of high recruitment in Cushing's (1975) match-mismatch hypothsis. Fishes with this strategy were termed "synchronous" by Sherman et al. (1984). An alternate

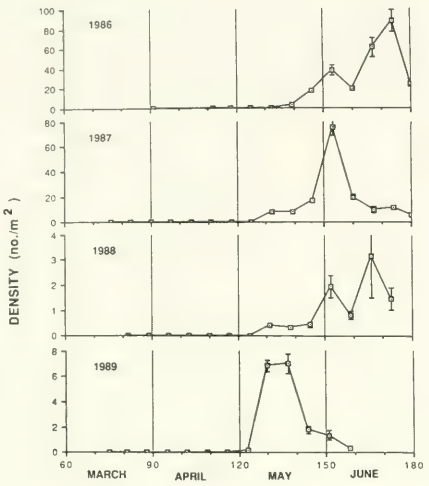

Figure 5

Mean densities of osmerid larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

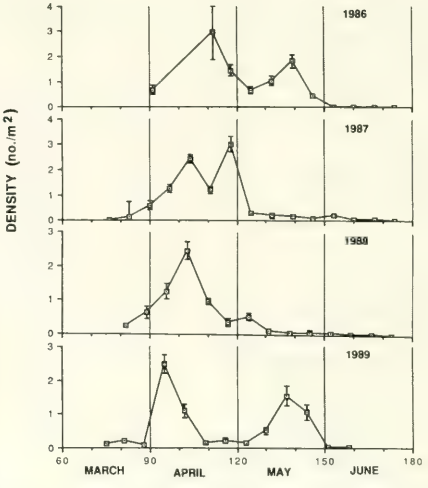

Figure 7

Mean densities of rock sole *Pleuronectes bilineatus* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

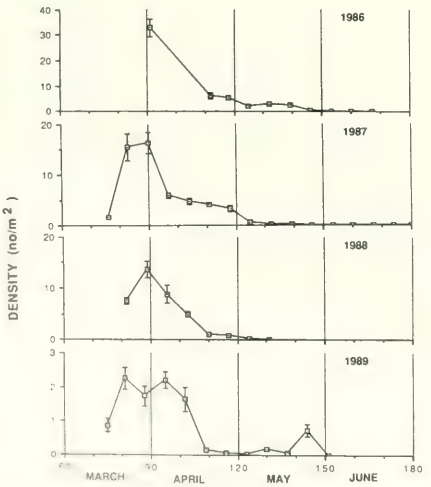

Figure 6

Mean densities of sandlance *Ammodytes hexapterus* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

strategy, characterized by prolonged production of larvae, has been termed "bet-hedging" (Lambert & Ware 1984) or "ubiquitous" (Sherman et al. 1984). This strategy is described as adaptive in situations where prey availability is unpredictable.

In Auke Bay, fish species reproducing in the spring appear to follow two strategies: One group, typified by walleye pollock and flathead sole, is clearly synchronous, in the sense described above; whereas Pacific sandlance and rock sole are examples of species that could be termed "early." The early group can be defined as those species that produce their larvae prior to the peak in the spring phytoplankton bloom (before mid-April in Auke Bay). It is possible that early species in Auke Bay are following the "bet hedging" strategy discussed above, as they could have been producing larvae throughout the winter. In that case our sampling would have coincided with the end of their production period.

From mid-March through June, conditions in Auke Bay are rapidly changing as the system passes through two of the production phases—spring phytoplankton bloom and herbivorous copepod maximum—that typify nearshore subarctic marine environments (Smetacek et al. 1984). In the pre-bloom period, the water column

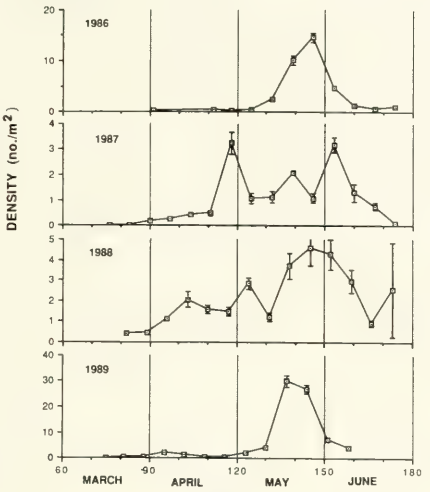

Figure 8

Mean densities of walleye pollock *Theragra chalcogramma* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

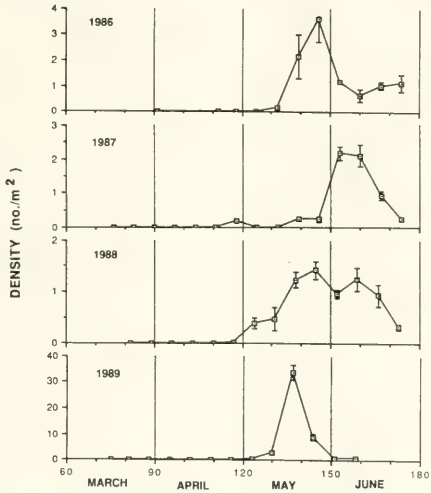

Figure 9

Mean densities of flathead sole *Hippoglossoides elassodon* larvae in Auke Bay, Alaska during spring and early summer, 1986-89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

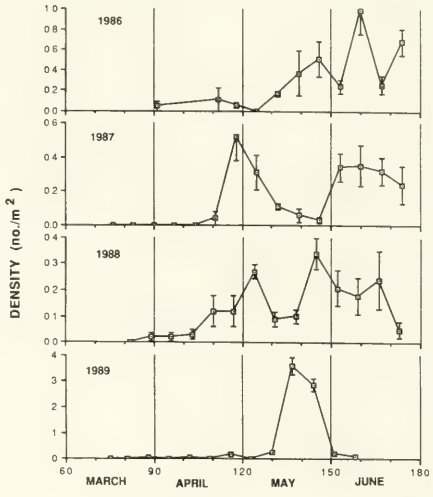

Figure 10

Mean densities of starry flounder *Platichthys stellatus* larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

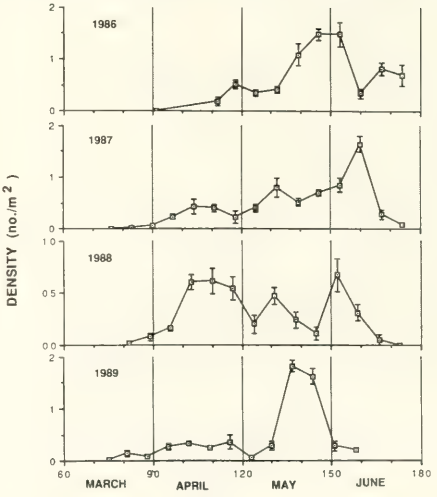

Figure 11

Mean densities of agonid larvae in Auke Bay, Alaska during spring and early summer, 1986–89. Error bars are 1SE; where no bars are visible, they are obscured by the point symbol.

is well mixed and uniformly cold, with mean temperature below 5°C. With onset of the phytoplankton bloom, the Bay stratifies, with rapid warming of the mixed layer to over 10°C by June (Bruce et al. 1977, Ziemann et al. 1991). Zooplankton are in low density until the end of the phytoplankton bloom, and are comprised of relatively large plankton such as overwintering copepedids and some meroplankton such as barnacle larvae (Wing & Reid 1972, Coyle & Paul 1990, Paul et al. 1991). The initiation of the herbivorous copepod maximum marks the start of a period with relatively high densities of smaller zooplankton, especially copepod nauplii in the size range (150–350 μ) utilized by synchronous species such as walleye pollock and flathead sole larvae (Fig. 12; data from Paul et al. 1991). It seems clear that fish larvae hatched prior to the phytoplankton bloom must be adapted to a very different set of conditions than those that occur synchronously with the herbivorous copepod maximum.

Larvae spawned in winter apparently employ various foraging strategies while utilizing similar energetic principles. Bailey (1982) concluded that Pacific hake larvae use energy slowly and grow slowly while passively hunting large prey. In Long Island Sound NY, larvae of American sandlance *Ammodytes americanus* hatched in winter are herbivores that survive nonfeeding in cold temperatures until the spring phytoplankton bloom commences (Monteleone et al. 1987). In both of these strategies, larvae survive by relying on their ability to withstand long periods of low food availability, largely as a result of low metabolic rates at cold temperatures.

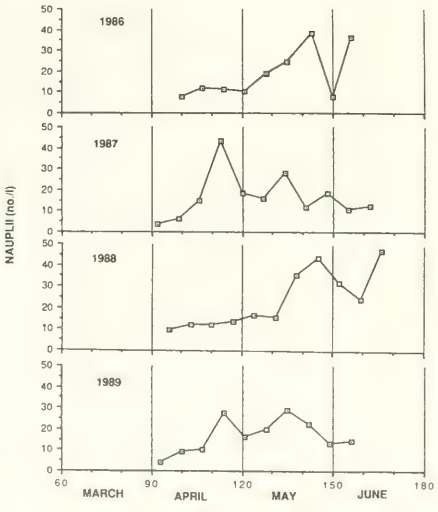

Figure 12

Densities of copepod nauplii (150–350μ) averaged over depths of 5, 10, and 15 m in Auke Bay, Alaska during spring, 1986–89 (data from Paul et al. 1991).

Sherman et al. (1984) identified the synchronous strategy as a major adaptive tactic for many northwest Atlantic Ocean fishes. In Auke Bay, several taxa including osmerids, walleye pollock, and flathead sole consistently appeared at about the time copepod abundance was maximized. Although prey is relatively plentiful during the herbivorous copepod maximum, the numbers of predatory invertebrates are rising (Smetacek et al. 1984, Coyle & Paul 1990); consequently, mortality rates of fish eggs and larvae are probably rising rapidly. Higher temperatures during this period may also limit the time available for larvae to encounter suitable conditions by causing high metabolic rates and more rapid depletion of energy reserves. These species are probably most sensitive to interannual variation in the production cycle and may demonstrate the type of recruitment fluctuation described by the match-mismatch hypothesis (Cushing 1975) or the critical-period hypothesis (Hjort 1914).

Patterns of abundance observed in Auke Bay could result from hatching of larvae in the Bay or from advective events that carried larvae into the Bay from other areas. Auke Bay has only one deep (>20 m) entrance, just east of Coghlan Island (Fig. 1). Water in the Bay is quite persistent, with an average replacement time of the water mass once a month or longer during the March–June period (Nebert 1990). In other studies of growth, length-frequencies were determined for walleye pollock and flathead sole larvae (Haldorson et al. 1989, 1990). Cohorts of both species first appeared in Auke Bay as small larvae comprising length-frequency modes that could be followed for several weeks. Over the 4 years of the study there were very few cases in which length-frequency modes occurred that could not be identified in preceding weeks. Consequently, we conclude that most of the larvae sampled in this study originated from hatching within or near the Bay, with possible exception of osmerids.

The osmerids in our study are most likely eulachon *Thaleichthys pacificus* and capelin *Mallotus villosus*. Eulachon is an anadromous species that spawns demersal, adhesive eggs in rivers. After hatching, the larvae are carried into nearby marine waters. The most likely source of eulachon larvae in Auke Bay is the Mendenhall River, a glacier-fed stream about 2 km east of Auke Bay. The fresh and turbid waters from the Mendenhall River form a surface lens that projects out into nearby Fritz Cove and often intrudes into the eastern edge of Auke Bay through a narrow passage

northeast of Spuhn Island (Fig. 1). In 1987 we studied the depth distribution of fish larvae in Auke Bay and found that osmerids were always concentrated above the pycnocline and moved to the surface at night (unpubl. data). Most other species were found at or below the pycnocline and tended to move deeper at night. Therefore, interannual and seasonal variation in osmerid abundance may reflect variation in the amounts of river water reaching Auke Bay.

Among the 4 years of the study, 1989 was distinguished by relatively high densities of larvae during May. Walleye pollock and flathead sole were markedly more abundant in 1989 than in the previous 3 years, as were less-common synchronous species such as starry flounder. This increase could have resulted from increased egg production in the bay or from exceptionally high survival of eggs and larvae. We have no data on density of fish eggs in Auke Bay; however, in 1989 invertebrate predators were present in the lowest abundance observed in the 4-year study (Coyle & Paul 1990). It seems possible that reduced predatory mortality contributed to the exceptionally high densities of fish larvae that occurred in May of 1989. However, 1986 also had relatively high abundances of fish larvae in May, and did not have reduced numbers of invertebrate predators (Coyle & Paul 1990).

Acknowledgments

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Age, growth, and reproduction of tautog *Tautoga onitis* (Labridae: Perciformes) from coastal waters of Virginia*

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Abstract–Tautog *Tautoga onitis* are gaining popularity in Virginia's coastal waters as a recreational and food fish. Adult tautog are seasonally abundant on inshore hardbottom habitats (1–10 m) and inhabit offshore areas (10–75 m) year-round. Juveniles, especially newly-settled recruits, inhabit vegetated areas in shallow water (usually <1 m). From March 1979 to July 1986, tautog were collected in lower Chesapeake Bay and nearby coastal waters to examine age, growth, and sexual maturation. Age estimates were determined from annular marks on opercle bones: 82% of the fish were age-10 or younger, 18% exceeded age-10, and 1% were age-20 or older. Marginal increment analysis revealed that annuli formed concurrent with a protracted spawning season (April–July). The von Bertalanffy growth equation, derived from back-calculated mean lengths-at-age, was l_t=742 $[1^{-e\,0.085\ (t-1.816)}]$. Tautog are long-lived (25+ yr) and attain relatively large sizes (672 mm TL) slowly (K for sexes combined = 0.085). Growth rates of both sexes are similar, although males grow slightly faster (K=0.090 vs. 0.085 for females). Maturity occurs at age-3 in both sexes. Growth rates for tautog from Virginia are similar to those reported nearly 25 years ago for tautog in Rhode Island. Growth rates for tautog are similar to those of other reef fishes, such as snappers and groupers. Habitat restriction, slow growth, great longevity, and increasing popularity by user groups may contribute to overexploitation of this species in Virginia waters.

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Fishery Bulletin, U.S. 91:45-64 (1993).

Tautog *Tautoga onitis* (Linnaeus) range from Nova Scotia (Bleakney 1963, Leim & Scott 1966, Scott & Scott 1988) to South Carolina (Bearden 1961, Sedberry & Beatty 1989) and are one of the northernmost-occurring labrids in the western North Atlantic (only the cunner *Tautogolabrus adspersus* ranges farther northward). Tautog are locally abundant in lower Chesapeake Bay from Gwynn's Island near the mouth of the Rappahannock River south to Sandy Point on the eastern shore (Hildebrand & Schroeder 1928), along hardbottom areas including those associated with the Chesapeake Bay Bridge-Tunnel network (CBBT) at the mouth of the Bay, and along the southern margin of the Bay near Lynnhaven Inlet. This species also occurs in coastal Atlantic waters off Virginia on hardbottom areas around jetties, and reefs and wrecks out to 65 km offshore (Richards & Castagna 1970, Musick 1972, Hostetter 1988). A wide size-range of tautog occurs from spring through late fall in the lower Bay and on the seaside coast; larger individuals occur year-round on suitable habitat offshore to 75 m and deeper. Newly recruited juveniles and young fish to about 100 mm usually inhabit shallow areas (1 m or less) densely vegetated with macrophytic algae (primarily *Ulva lactuca*) or submerged seagrasses including stands of *Zostera* and *Ruppia* (Briggs & O'Connor 1971).

In more northern regions, a marked decrease in activity of tautog has been observed to occur in water temperatures below 10° C (Olla et al. 1974). Smaller individuals overwinter in shallow, rocky areas, whereas when autumn temperatures fall below 10° C, larger and older fish (>25 cm, >3–4 yr old) migrate to offshore, overwintering areas. Adult tautog return from offshore wintering areas to inshore spawning sites with onset of increasing temperatures in the spring (Chenoweth 1963, Cooper 1966, Stolgitis 1970, Olla et al. 1974, Briggs 1977, Olla et al. 1979). In Virginia, tautog populations on nearshore sites also undergo seasonal fluctuations. However, seasonal movements of tautog in Virginia's coastal waters may not be as well defined as the migration patterns noted for tautog in more northern areas. In our study area, not all tautog migrated to inshore areas during

* Contribution 1758 of the Virginia Institute of Marine Science, College of William & Mary.

springtime spawning periods. Tautog in peak spawning condition were collected on both inshore and offshore sites throughout the spring-summer period (late April–early August). Additionally, it was not unusual to observe large fish (>25 cm) at inshore sites during winter, especially in deeper areas. In more northern areas, other researchers (Olla & Samet 1977, Eklund & Targett 1990) have also noted that some adult tautog in the population remain offshore throughout the year.

Tautog are rapidly gaining popularity as a prized food and sport fish with recreational anglers and spearfishermen in Virginia waters (Bain 1984, Arrington 1985). Recreational angling for this species in Virginia has received increased interest since the recent capture of a world record tautog (24 lb, 10.89 kg) by an angler fishing off the eastern shore of Virginia (IGFA 1990). This increasing popularity has also been reflected in the number of awards issued annually to recreational fishermen by the Virginia Salt Water Fishing Tournament for outstanding catches [tautog weighing 4.1 kg (9 lbs) or more]. Awards for outstanding catches of tautog increased from mean values of 122/yr for the period 1976–80 to 282/yr for 1981–86 (C. Bain, Virginia Saltwater Fishing Tournament, VMRC, Virginia Beach VA 23451, pers. commun.). Most recently, however, citations for outstanding catches have decreased to 106/yr (range 91–130/yr) for 1987–91. Commercial catches from 1922 (Hildebrand & Schroeder 1928) to the present (E. Barth, Deputy Chief, Fish. Manage. Div., VMRC, Newport News VA 23607, pers. commun. 3 Jan. 1991) show little annual variation in weight of reported catches in landings for this species. Reported commercial landings of tautog in Virginia from 1973 to 1988, for example, ranged from 234 to 3586 lb/yr ($\bar{x}$=1840 lb/yr). However, these landings are insignificant compared with unreported catches by commercial and recreational rod-and-reel fishermen. According to statistics compiled by the Marine Recreational Fishery Statistics Survey conducted by the National Marine Fisheries Service (NMFS), estimated recreational catches of tautog in the mid-Atlantic Bight from 1979 to 1989 ranged from 70,000 (1982) to 815,000 (1984) fish/yr ($\bar{x}$=383,200 fish/yr). In 1985, landings of tautog taken by recreational anglers in Virginia alone were estimated to be 743,600 lb, representing 3.6% of the total estimated poundage for fishes taken by recreational fishermen in Virginia (VMRC 1985).

Aspects of the tautog's biology, including its association with hardbottom areas (Bigelow & Schroeder 1953, Cooper 1967, Olla et al. 1974, 1977, 1979), which are limited and generally discontinuous in Virginia, and its relatively slow growth (Cooper 1967), render this species susceptible to overexploitation (Briggs 1977). This situation is further exacerbated by recent technological advances in LORAN and recording depth finders used by fishermen that have simplified locating even the smallest, isolated substrates. Populations of slow-growing fish species concentrated in reef areas can be severely depleted by fishing pressure exerted by recreational interests (Briggs 1977, Turner et al. 1983, Manooch & Mason 1984, Matheson and Huntsman 1984, Moore & Labisky 1984, Harris & Grossman 1985). Based on informal surveys of charterboat captains, recent declines in citation awards for large fish, and personal field experiences, the catch-per-unit-effort of tautog has already decreased in Virginia, and the relative abundance of tautog (especially larger-sized individuals) has been detrimentally affected in the more popular fishing areas.

In coastal waters of Rhode Island and New York, Cooper (1966), Olla et al. (1974), and Briggs (1977) noted a seasonal inshore-offshore spawning migration in tautog with no significant north-south component. None of these studies reported the recovery of fish from areas outside the general area in which they were tagged, indicating that little, if any, mixing of adult tautog takes place between fish inhabiting even relatively proximate areas (Rhode Island and New York waters).

This study was undertaken to estimate age structure of the population, growth, longevity, and seasonal patterns of reproduction for tautog occurring in lower Chesapeake Bay and nearby coastal waters of Virginia. Growth parameters estimated for tautog collected in Rhode Island 25+ years ago may not be applicable for the population(s) occurring in more southerly waters. Also, in coastal waters of Rhode Island and Virginia where tautog occur, environmental parameters (primarily seasonal temperature regimes) and habitat availability are different, and these factors may influence growth rates in different populations or segments of the same population. Occurrences of large specimens, such as the current (IGFA 1990) and previous (IGFA 1986) world-record tautogs in coastal waters of Virginia, may also indicate that fish in the lower Mid-Atlantic Bight comprise a separate population, with growth characteristics different from their northern counterparts.

Materials and methods

Tautog were collected opportunistically from March 1979 to July 1986 by spearfishing, rod-and-reel, commercial fish pots, and as bycatch in trawl tows from other research studies. During the course of the study, fish were taken at 19 different locations, at depths of 2–35 m and representing a wide variety of ecological conditions characteristic of tautog habitat within

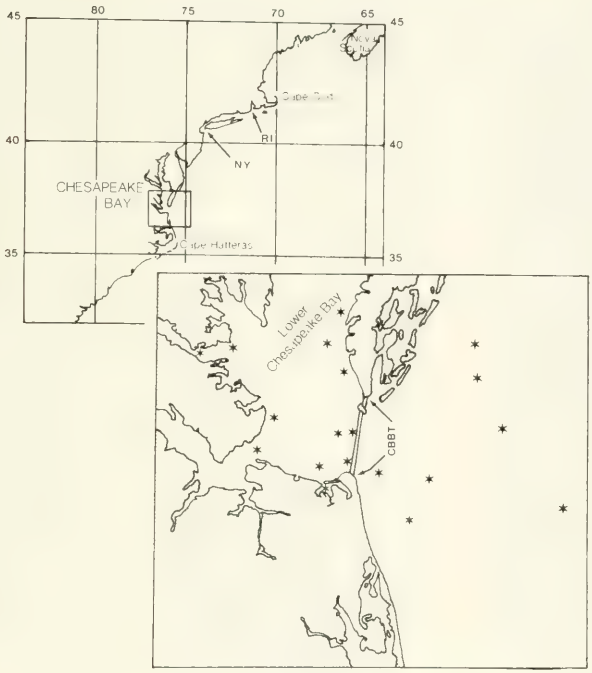

Figure 1

Collection localities (marked by stars) in lower Chesapeake Bay and Virginia coastal waters where *Tautoga onitis* were collected for age, growth, length, and weight parameters. Stars indicate general collecting areas, with most indicating more than one collection per area. Arrows indicate locations of the Chesapeake Bay Bridge Tunnel (CBBT) and of previous studies on tautog from Rhode Island (by Cooper, see Citations) and from New York and northern New Jersey (by Briggs & Olla and co-workers, see Citations).

Chesapeake Bay and offshore hardbottom areas (CBBT, wrecks, artificial reefs) of coastal Virginia (Fig. 1).

Each specimen was measured to the nearest 1 mm for standard length (SL) and total length (TL), and weighed (WT) to the nearest 5 g. Length data from both sexes were combined to generate a regression equation for SL on TL (TL = 4.78+1.20 SL). High correlation (r^2=0.98) between these measurements prompted the use of TL in analyses, since this was the more easily and reliably obtained measurement.

For each fish, an initial determination of sex was made by examining several external characters that have been previously shown to be dimorphic (Cooper 1967, Olla & Samet 1977). Adult males usually have a blunt forehead with a more massive mandible, compared with that of adult females which have a less massive mandible and more anteriorly-tapered profile of the head. Larger males are typically gray and have distinctly visible (especially underwater) white markings on the caudal, pelvic, and dorsal fins, and also on the chin region. Females (all sizes) and smaller males tend to have a mottled brown coloration without white markings on the fins and chin region.

After initial determination of sex based on external characteristics, gonads were then excised, staged macroscopically for maturity state, and weighed (gonad weight = GW) to the nearest 0.1 g (gonad weights were not available for all fish). Maturity stages were defined as follows: **Immature**—gonads undifferentiated; **Mature**—gonads obviously differentiated; **Ripe**—gonads enlarged, containing sperm or ova; **Running ripe**—sperm or ova expressed when slight pressure applied to abdomen; **Spent**—large, flaccid gonads, often bloody in appearance, with no obvious signs of sperm or ova upon dissection. A gonadosomatic index (GSI) for females for all years combined was calculated using the formula GSI=GW × 100/WT.

Scales, saccular otoliths, and opercles were collected and compared to determine the best method for ageing tautog. Whole unsectioned opercles (Fig. 2) were prepared following procedures used by Cooper (1967). The articular apical center, as defined by Le Cren (1947), McConnell (1952), Bardach (1955), and Cooper (1967), is the center of the high ridge projecting from the medial surface of the opercle. Opercular radius (OR), defined as the distance from the articular apex center to the midpoint of the posterior margin of the opercle, was measured with dial calipers to 0.1 mm (Fig. 2). Similarly, measurements (to 0.1 mm) were made along this axis to each annulus to determine annual growth increments. An annulus was defined as the sharp transition from a translucent (hyaline) to an opaque zone on the opercle. Only discernible annuli continuous from

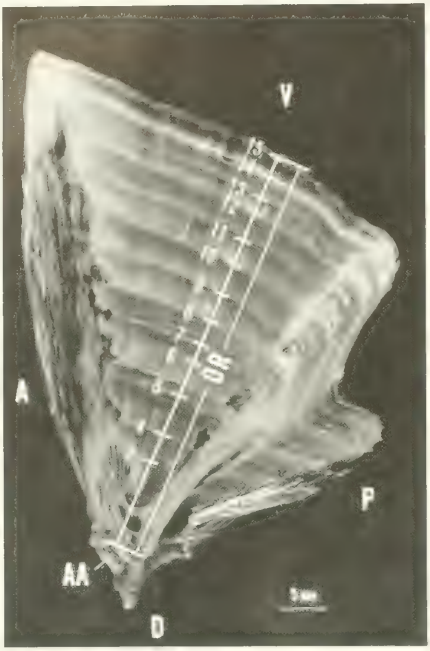

Figure 2

Measurements on each opercle of *Tautoga onitis* used in age analyses. Illustration depicts whole left opercle from *Tautoga onitis*. Orientation of the opercle is: **(A)** anterior; **(P)** posterior; **(D)** dorsal; **(V)** ventral. Successive annuli (3–15; first two annuli obscured by articular apex) are indicated; **OR** is the opercular radius; **AA** is the articular apex of the opercle.

anterior to posterior margins of the bone were considered to be annuli and counted to determine age. Other horizontal marks such as incomplete bands (= false checks) were not included in the annuli counts. All annuli continuous within contours of the opercle were counted on both right and left opercles using transmitted light. Initially, annuli on both opercles from each fish were counted with 90% agreement between counts. If differences were noted, the age estimate from the opercle with the most clearly defined annuli was used. All age estimates were made by the senior author, then a subset (n=100) of those opercles were re-read by the second author. All initial estimates by both readers were in agreement, thus age estimates (by Hostetter) were used in subsequent analyses.

Annuli were counted for both right and left opercles using transmitted light. A total of 24% (167/706) of the opercles were counted six times; four counts were made at 1× and two were made at 6× magnification. Since there was close agreement between all counts regardless of magnification, the remaining 76% of opercles were aged twice under 1× magnification. Marginal increment, the seasonal growth of the opercle, was measured by plotting increment width from the last annulus (A) against date of capture (Fig. 3).

Standard least-squares linear regression (Sokal & Rohlf 1981) was used in Lotus-R spreadsheet format (Jeanty 1984) to describe TL:SL, TL:OR, and TL:WT relationships. Determination of time of annulus formation was adopted from Nose et al. (1955) and Cooper (1967). Mean back-calculated TL-at-age (Table 1) was computed for males and females separately and for sexes combined, following Bagenal & Tesch (1978). Slope and intercept values from these equations were used in the back-calculated length equation of Ricker (1975). Calculated lengths by sex were independently determined through substitution of logarithmic values for average TL and OR by age-class. Analysis of covariance (ANCOVA) using SPSS-X (Norusis 1985) was used to compare age-at-length between sexes. Back-calculated mean lengths-at-age were used to develop von Bertalanffy curves (Gulland 1976).

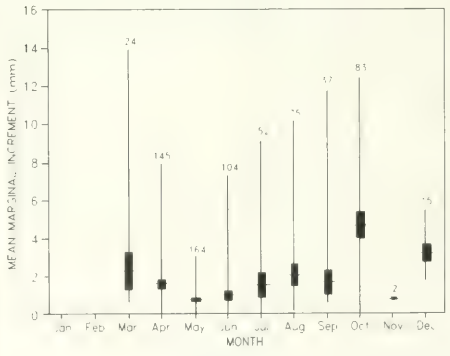

Figure 3

Mean seasonal incremental growth (in mm) of opercles of *Tautoga onitis* from coastal waters of Virginia. Vertical bars represent the range; middle horizontal bars are the mean; darkened portions represent the standard deviation; and numbers at top of each line are sample sizes.

Table 1

Back-calculation formulae for male and female *Tautoga onitis* from coastal waters of Virginia (TL=mm total length; OR=mm opercular radius); L_n=total length at year n; R_n=opercle radius at year n; R_t=opercle radius at capture; b=slope of body-bone regression; where $L_n = \log TL + b(\log R_n - \log R_t)$.

(males) log TL = 1.2916+0.860 log OR (n=398; r^2=0.968)
(females) log TL = 1.2889+0.864 log OR (n=281; r^2=0.967)

Results

Ageing technique and validation

Opercles were found to be the best structure for estimating age of tautog. In fish with less than four annuli, there was close agreement between annuli on scales and those on opercles. However, abrasion, surface-area damage, and ring compaction along the outer margin of scales precluded using scales for ageing older fish. Comparisons of age estimates from otoliths and opercle bones from 27 fish indicated close agreement in readings of annuli from each structure, especially in younger fish. However, otoliths from larger fish had a thickened nuclear core, which made it difficult to discern any microstructure in this region. Sanding and sectioning of otoliths proved difficult because of the small size of the otoliths, and in most cases these procedures also blurred or removed annuli on the outer edge of the otolith. The first annulus is also sometimes difficult to detect on opercles of large tautog because of thickening of the buttress zone at the articular apex. In these instances (<5% of the fish aged), we assigned a distance to the first annulus (7.4 mm) based on mean measurements from opercles with clearly defined first annuli.

Opercle radius and TL (Fig. 4) were linearly related (r^2=0.97; sexes combined). Age estimates based on the first and fourth readings (at 1×) of individual opercles were in close agreement (81%, 135/167). All age disagreements were within 1yr (n=31), except one (2 yr).

Marginal increment analysis (Fig. 3) revealed minimum growth distal of the last annulus during May, June, and early July for all age-groups. There was no indication of formation of a second mark during the year for any fish examined.

Age and growth

A total of 712 tautog measuring 51–765 mm TL was collected (Fig. 5). Of these, 701 (398 males, 282 females, and 21 immature fish of unknown sex) were used to estimate age distribution and growth rates.

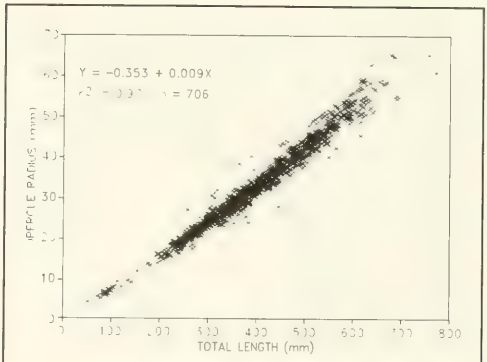

Figure 4

Relationship of opercular radius (OR) on total length (TL) for *Tautoga onitis* (sexes combined) from coastal waters of Virginia, 1979–86.

Specimens not included in age analyses had missing data or damaged opercles, which precluded their use in the analyses. Mature males (n=364) ranged in size from 198 to 765 mm TL, weighed 138–6895 g, and were aged 3–25 yr. Mature females (n=247) were comparable in size (232–750 mm TL) and weight (130–7392 g), and were aged 3–21. Few males (9%, n=32) and females (5%, n=14) in our samples were older than age-13. Immature fish ranged from 51 to 265 mm TL, weighed 5–410 g, and were aged 0–3 yr. Length-weight relationships (Figs. 6,7), calculated separately for males and females, indicated that mean total lengths and

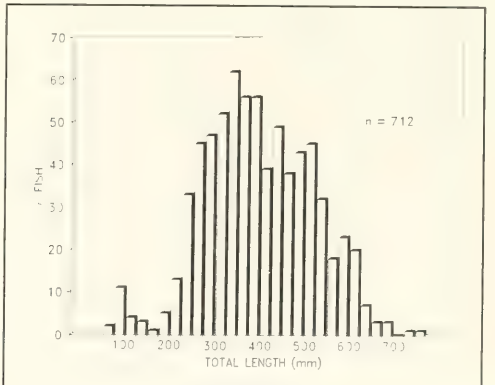

Figure 5

Length-frequencies of *Tautoga onitis* within 25 mm TL size-classes collected in coastal waters of Virginia, 1979–86.

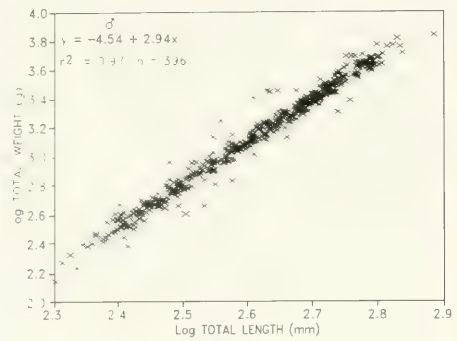

Figure 6

Length-weight relationship for male *Tautoga onitis* collected in coastal waters of Virginia, 1979–86.

weights (Tables 2,3) increased with age for both sexes ($P<0.01$).

Estimates of mean back-calculated size-at-age (Tables 4,5) suggest that growth for male and female fish is similar. However, we analyzed the data by sex to compare with previously reported values. Greatest incremental growth in TL for both sexes occurred during the first year and then declined rapidly. Growth in the second year was only 40–49% of that recorded for the first year for both sexes (Tables 4,5). Only small differences in back-calculated lengths-at-age occurred between the sexes to age-13 (Tables 4,5), and these were not statistically significant. Males usually had a slightly larger growth increment at each successive age throughout the life span.

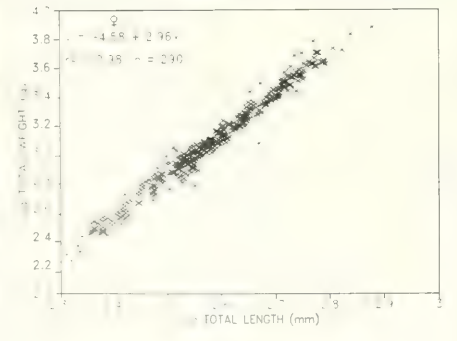

Figure 7

Length-weight relationship for female *Tautoga onitis* collected in coastal waters of Virginia, 1979–86.

Estimates of empirical length-at-age (Table 6) compared favorably with both back-calculated estimates (Tables 4,5) and observed growth (Tables 2,3). K-value for male tautog (0.090) was greater (Table 6) than that calculated for females (K=0.085). Males were also larger in size (TL) when compared with females of comparable age (Fig. 8), although the differences were not statistically significant. Males and females achieved 50% of L_∞ between ages 6 and 7, and 75% between ages 14 and 15. ANCOVA analyses indicated no significant differences between slopes of regression equations of length-at-age for male and female tautog (F=2.600, $P>0.05$) or for homogeneity of means around regression slopes (F=2.979, $P>0.05$).

Derived length-at-age estimates from von Bertalanffy growth equations were later used in regression equations to calculate weight-at-age. Although correlation coefficients were high (r=0.81) in the analysis of WT on TL, variation in weight-at-age within age-groups was considerable, and estimates of growth based on weight were less reliable than estimates based on TL.

Sexual dimorphism and reproductive biology

We observed two different morphological males in fish we examined. Approximately 15% of the fish we classified initially as females, based on external characteristics, were later determined upon dissection to be males. Generally, these non-dimorphic males were fish smaller than 550 mm TL and less than age-10. However, several approached the largest sizes observed for other males. Pigmentation of non-dimorphic males was a dull mottled brown, with remnants of disrupted lateral bands, and was similar to that noted for females. In contrast, dimorphic males were typically grayish with distinctive white markings on ventral and dorsal margins of pectoral and caudal fins and on the chin. The anterior skull and rostral region were also blunter and more massive in dimorphic males than for those noted in females and non-dimorphic males. Both types of morphological males were considered as males in analyses of age and growth and sex ratios.

Gonadal maturation was evident in both sexes by age-3. Age-2 fish, collected only in late March and early April, were immature with undeveloped gonads. GSI values for females plotted against date of capture (Fig. 9) indicated peak spawning from April through June, with the highest GSI recorded in May. GSI values declined rapidly after July. Although not shown, the GSI of tautog collected inside and at the mouth of Chesapeake Bay peaked somewhat earlier, in mid-May, and started to decrease by mid-June, whereas a small percentage (usually ~20%) of running ripe fish were

Table 2

Sample sizes (n), means ($\bar{x}$), and standard deviations (SD) for total and standard lengths (mm), and weight (g) by age for male *Tautoga onitis* from coastal waters of Virginia.

	Total length			Standard length			Weight		
Age	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1	11	246	21	11	201	17	11	306	98
2	23	276	33	23	225	28	22	491	156
3	52	292	40	52	240	33	51	542	261
4	38	329	42	38	273	41	34	740	306
5	29	357	57	29	295	47	27	982	459
6	30	375	46	30	313	43	30	1145	447
7	31	414	52	31	340	52	31	1577	711
8	40	443	42	40	364	34	40	1795	511
9	39	481	47	39	398	47	39	2397	694
10	30	501	48	30	416	48	30	2693	794
11	18	533	41	18	438	36	18	2911	731
12	20	564	47	20	466	38	20	3663	839
13	6	545	22	6	451	22	6	3410	466
14	7	574	25	7	474	23	7	3861	573
15	1	595	0	1	491	0	1	4340	0
16	5	586	29	5	489	30	5	4202	777
17	2	587	27	2	479	20	2	4860	30
18	8	655	48	8	532	31	7	5549	766
19	3	614	15	3	504	10	3	4452	62
20	1	550	0	1	460	0	1	3090	0
21	1	613	0	1	508	0	1	4750	0
22	2	655	25	2	538	22	2	4995	725
23	0	—	—	0	—	—	0	—	—
24	0	—	—	0	—	—	0	—	—
25	1	672	0	1	577	0	1	6568	0

Table 3

Sample sizes (n), means ($\bar{x}$), and standard deviations (SD) for total and standard lengths (mm), and weight (g) by age for female *Tautoga onitis* from Virginia.

	Total length			Standard length			Weight		
Age	n	x	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1	12	224	33	12	185	28	12	256	107
2	23	268	37	23	222	32	23	444	182
3	31	286	40	31	236	33	31	526	240
4	34	334	30	34	274	26	34	822	226
5	27	350	35	27	284	33	27	910	245
6	23	378	47	23	317	44	23	1205	468
7	37	401	38	37	334	33	37	1395	479
8	16	425	43	16	351	38	16	1551	438
9	20	453	58	20	375	46	20	1960	700
10	13	519	42	13	428	37	13	3114	876
11	13	524	54	13	436	46	13	3033	873
12	11	545	42	11	451	35	11	3660	1063
13	8	525	39	8	437	31	8	3227	643
14	3	551	64	3	464	54	3	3677	1188
15	2	518	30	2	429	20	2	2715	395
16	1	485	0	1	395	0	1	2530	0
17	1	575	0	1	479	0	1	4220	0
18	5	628	80	5	517	47	5	4961	1700
19	0	—	—	0	—	—	0	—	—
20	1	557	0	1	485	0	1	3385	0
21	1	660	0	1	570	0	1	5100	0

Table 4

Back-calculations of growth (mm) for male *Tautoga onitis* from coastal waters of Virginia.

Age (yr)	No. of Specimens	Mean length at capture	Mean back-calculated lengths at preceding annuli																							
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	11	174	123																								
2	23	252	144	219																							
3	52	288	147	216	268																						
4	38	325	141	203	262	308																					
5	29	353	141	199	253	303	341																				
6	30	379	144	202	254	296	332	362																			
7	31	418	152	210	254	301	342	377	409																		
8	40	440	151	204	251	292	329	367	404	431																	
9	39	477	152	203	257	300	340	375	409	441	469																
10	30	501	145	204	251	298	337	370	403	433	464	491															
11	18	519	171	197	242	279	310	346	375	404	433	460	502														
12	20	560	139	194	248	295	338	376	412	444	476	509	533	554													
13	6	561	147	195	250	284	316	344	370	400	432	465	499	528	551												
14	7	566	145	188	241	294	329	362	391	421	447	473	497	523	546	562											
15	1	592	154	204	226	264	307	348	368	400	433	459	486	514	552	570	586										
16	5	578	153	201	260	286	313	328	358	383	406	435	462	490	511	532	550	569									
17	2	593	147	203	259	287	321	344	363	394	417	445	460	481	510	531	554	574	588								
18	8	668	154	209	244	275	310	344	377	413	449	485	512	542	570	595	614	636	652	664							
19	3	615	127	173	229	264	298	330	352	373	397	423	446	472	502	521	543	558	574	597	612						
20	1	578	131	156	209	239	272	300	326	352	374	394	418	445	467	492	514	533	544	553	564	575					
21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
22	2	622	118	165	218	243	268	289	327	358	390	431	452	473	495	508	528	546	564	579	593	606	614	622			
23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
24	1	679	164	204	232	267	290	311	349	380	411	437	463	481	505	529	561	586	605	616	629	643	650	658	666	673	
25	1	672	119	182	236	272	296	322	339	357	375	393	406	435	465	491	519	558	586	611	631	641	648	655	662	668	672
Weighted mean			146	204	254	296	331	364	397	425	452	475	499	522	531	547	563	581	599	616	602	608	632	639	664	671	672
Growth increment			146	58	50	41	36	33	33	28	28	23	24	23	9	16	16	18	18	18	–14	6	24	7	26	7	1

Table 5

Back-calculations of growth (mm) for female *Tautoga onitis* from coastal waters of Virginia.

Age (yr)	No. of Specimens	Mean length at capture	Mean back-calculated lengths at preceding annuli																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	23	174	123																			
2	28	249	131	212																		
3	31	288	130	202	263																	
4	32	333	138	208	260	312																
5	29	345	133	200	249	296	332															
6	24	379	137	196	251	294	340	368														
7	34	401	135	192	244	283	322	360	387													
8	19	422	134	195	248	292	326	358	389	412												
9	21	450	146	207	254	293	328	358	388	420	443											
10	10	522	144	206	261	298	340	378	409	445	481	508										
11	14	522	137	193	245	294	335	373	404	430	460	486	513									
12	9	527	134	189	240	278	311	349	379	404	431	461	492	515								
13	12	540	134	196	250	285	319	344	370	397	426	452	483	508	530							
14	2	558	157	205	246	312	368	400	422	447	466	489	506	525	542	555						
15	2	513	126	169	235	265	286	316	339	363	385	404	434	455	474	490	505					
16	2	516	122	164	227	245	263	284	304	331	360	384	416	434	455	476	497	512				
17	1	575	112	193	237	259	281	309	340	367	380	414	432	467	490	508	535	548	566			
18	4	614	127	175	222	251	288	320	347	373	402	430	458	484	507	534	554	577	592	608		
19	1	685	150	223	275	325	384	413	440	452	470	504	530	565	585	608	626	643	662	676	683	
20	1	557	164	192	230	245	258	279	297	313	336	355	371	393	413	433	456	487	506	527	543	550
21	1	660	148	180	216	266	310	354	390	437	476	502	526	545	560	572	588	594	600	621	634	645	660
Weighted mean			134	200	251	292	327	359	386	413	440	466	486	499	515	521	536	560	587	608	620	598	652
Growth increment			134	65	51	41	34	32	27	27	28	26	19	13	16	7	14	25	27	21	12	–22	55

Table 6

Estimated parameters and standard errors (SE) of the von Bertalanffy growth equation for *Tautoga onitis* from coastal waters of Virginia (L_t=mean asymptotic total length in mm; K=growth coefficient; t_0=time (yr) at which total length would theoretically be zero).

Parameter	Estimate	Asymptotic SE
Males		
L_t	732.24	9.124
K	0.090	0.003
t_0	−1.64	0.132
Females		
L_t	733.61	28.362
K	0.085	0.009
t_0	−1.74	0.324
Sexes combined		
L_t	742.37	9.051
K	0.085	0.003
t_0	−1.816	0.144

present in samples from offshore collecting sites until late July and early August. Fish occurring on wrecks further offshore (and usually deeper) generally had higher GSI values later into the season (early July–early August) than those collected from inshore areas.

Chi-square analysis of sex ratios for 701 tautog divided into 10 cm length-groups indicated significant deviations (χ^2=18.87; df=1) from a 1:1 sex ratio in the larger size-classes (Table 7). The larger size-classes and older fishes were comprised predominantly of males.

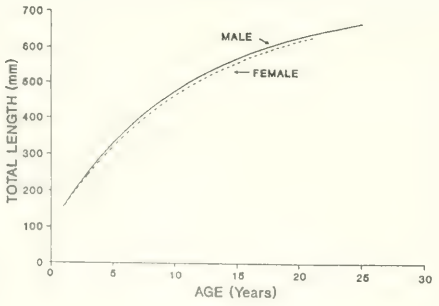

Figure 8

von Bertalanffy growth curves for male and female *Tautoga onitis* collected in coastal waters of Virginia, 1979–86.

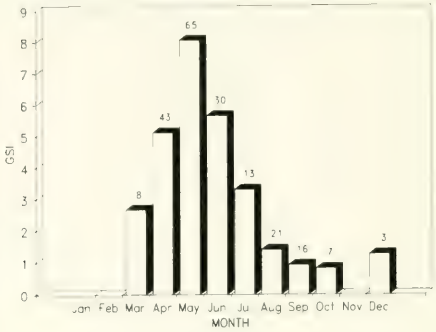

Figure 9

Seasonal gonadal development (gonadosomatic index, GSI) for female *Tautoga onitis* collected in coastal waters of Virginia, 1982–84. Numbers over bars are sample sizes.

Discussion

Age and growth

The only previously published study on age, growth, and longevity of tautog was from samples collected in and near Narragansett Bay, Rhode Island (Cooper 1967). Cooper's (1966) tag and recapture data verified that continuous rings on opercle bones in tautog represented annuli and that these marks were indicative of rate of growth over the year. High level of agreement between opercle readings, high linear correlation between TL and OR, and consistent time of annulus formation for fish examined in this study were similar to results reported by Cooper (1967).

Our study is the first to present information on growth and longevity for tautog from southern portions of the species range. Our results agree with those of Cooper (1967) on tautog from Rhode Island that the

Table 7

Chi-square analysis of sex ratios for different size-classes of *Tautoga onitis* captured in coastal waters of Virginia (*P 0.05= 3.84; **P 0.01=6.63).

Standard length (mm)	Male	Females	χ^2	P
0–100	16	24	1.60	NS
101–200	137	110	2.95	NS
201–300	128	94	5.21	*
301–400	103	57	13.23	**
401–500	24	8	8.00	**

tautog is a long-lived species that reaches relatively large sizes slowly. Seasonal growth, reflected by annular growth increments on opercles (Fig. 3), is one of rapid somatic growth following spawning, with maximum yearly growth achieved from July to December. Slower rates of somatic growth during January to March may be attributed to decreased feeding during colder winter temperatures (Cooper 1966, Olla et al. 1974). From March to June, the rate of somatic growth is less than that observed in other seasons and most likely results from energy expenditure associated with gonadal maturation and spawning.

In Virginia and Rhode Island, annual growth in length was rapid during the first three years (~33% and 38% of the total in Virginia and Rhode Island, respectively) and declined steadily with increasing age. Except for age-1, annual growth increments between populations were roughly similar to about ages 12–13, after which yearly increments (TL) in Rhode Island fish declined rapidly; whereas growth rates for tautog of the same age-groups from Virginia's coastal waters did not diminish as rapidly. In fact, from about ages 12–13 onward, annular growth increments of tautog from Virginia were nearly double those of their counterparts from Rhode Island (compare Tables 4&5 with Cooper 1967). Other differences between this study and Cooper's (1967) are that tautog in Virginia reach twice the TL of those in Rhode Island at time of first annulus formation. Annular growth estimated by back-calculations indicated that in tautog from Virginia, the greatest average yearly increment in growth occurred during the first year. In contrast, Cooper found that both sexes had their largest yearly increase in TL during their second year of life. Observed differences in first-year growth of tautog from Virginia and Rhode Island result either from our missing the first annulus, or from differences in environmental factors between study areas. We discounted missing the first annulus, because we believe we had adequate numbers of fish in these younger age-groups (n=204), from both seasonal and size perspectives, to consider this a reasonable estimate of opercle size at age-1. Additionally, back-calculated lengths-at-age-1 for all tautog aged closely matched actual observations of TL at the end of the first year (compare Tables 2,3 and 4,5).

Observed differences in first-year growth between tautog occurring in Virginia and Rhode Island may result from environmental factors in more southern waters that favor growth over a longer season (Fig. 10). For example, temperatures in shallow-water areas below which juvenile tautog become inactive (~10° C) occur earlier and persist longer in inshore coastal waters of Narragansett Bay, Rhode Island than in the lower York River in Chesapeake Bay. On average, water temperatures in springtime remain below

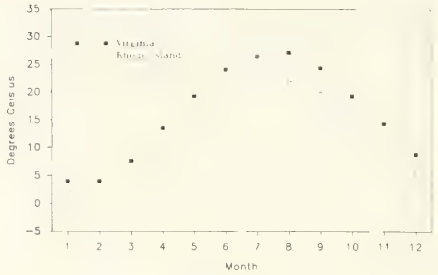

Figure 10

Average monthly water temperatures (1979–86) for lower York River, Virginia (VIMS oyster pier, taken 1m below surface at 2.0–2.5m depth; G. Anderson, Coll. William & Mary, VIMS, Gloucester Point VA, pers. commun.), and for bottom-water temperatures at Fox Island, Narragansett Bay, Rhode Island (H.P. Jeffries, Univ. Rhode Island, Grad. School Oceanogr., Narragansett RI, pers. commun.). Solid squares and open triangles represent mean monthly values for York River and Narragansett Bay, respectively.

10° C nearly a full month longer in Narragansett Bay (not until mid-April) than in the York River (usually mid-March). And in the fall, temperatures again decline below 10° C during mid- to late October in Narragansett Bay, whereas in Virginia temperatures remain above 10° C usually well into mid-November or early December. These temperatures, which are conducive for somatic growth in juvenile tautog, are extended seasonally in coastal waters of Virginia compared with those of more northern areas. Recently, D.L. Martin and T.E. Targett (Grad. Coll. Mar. Stud., Univ. Delaware, Lewes DE 19958, unpubl. data) found in laboratory growth experiments that young-of-the-year tautog from high-latitude populations (Rhode Island) show no genetic compensation for a shorter growing season when compared with tautog from Delaware Bay and Virginia waters. These data further support our hypothesis that observed differences in growth of young tautog from northern (Rhode Island) and southern (Virginia) areas of the species range are due primarily to environmental factors between the two areas (i.e., duration of optimal temperatures for growth is longer in Virginia coastal waters compared with those of coastal areas in the northern end of the species range).

Estimated values of L_∞ for tautog from Virginia are also considerably higher than those estimated for tautog from Rhode Island (Table 8). A calculated L_∞ of 733 mm TL (data for sexes combined; 733 mm for females, 732 mm for males) as derived from the von Bertalanffy equation in our study is close to the observed maximum TL of 765 mm. Growth equations es-

Table 8

von Bertalanffy growth functions derived for *Tautoga onitis* collected in Virginia (1979–86) and Rhode Island (from Cooper 1965).

Virginia tautog			
(males, n=398)	K	=	0.090, L_∞ = 732
	t_o	=	−1.644
	L_t	=	$732[1-e^{-0.090(t+1.644)}]$
(females, n=281)	K	=	0.085, L_∞ = 733
	t_o	=	−1.743
	L_t	=	$733[1-e^{-0.085(t+1.743)}]$
Rhode Island tautog			
(males, n=1041)	L_t	=	$664[1-e^{-0.091(t+1.062)}]$
(females, n=1119)	L_t	=	$506[1-e^{-0.118(t+0.952)}]$

timated for tautog in Rhode Island (Cooper 1965) indicated appreciably smaller L_∞ values (506 mm and 664 mm) for both sexes compared with those estimated for tautog in Virginia.

The present study also found that males grow at a somewhat faster rate than females. Cooper (1965) found a slightly faster growth rate in females when compared with males (Table 8). However, in both studies estimated K-values are comparable. Similarities in K-values between tautog occurring in Rhode Island and Virginia support the contention that growth rate (K) is an intrinsic value for the species, largely independent of geographic location.

Although Cooper (1965) found that females initially grew at a faster rate than males, he reported divergence in growth between sexes favoring faster growth in males after age-3. We also found similar divergence in growth of males, but unlike Cooper's study, this difference was apparent for males at all ages.

In our study area, males live longer than females. The oldest fish examined were a male estimated to be age-25 and a female estimated to be age-21. Cooper (1967) indicated a life span of 34 yr for males and 22 yr for females in the population he studied in Rhode Island, and suggested that females may reach senescence at an earlier age than males. Although longevity estimates of tautog based on actual data range between 25 and 34 yr, most fish aged were considerably younger than this, and it seems that claims of fish more than a half century old (Reiger 1985) are exaggerated. Average age for tautog in this study was just over 7 yr; 82% of the fish were age-10 or younger, only 1% were age-20 or older. Cooper (1967) found a similar age structure in the population of tautog residing in Narragansett Bay just over 25 yr ago, where approximately only 15% and 8% of males and females, respectively, were older than age-13. The current world record for tautog (IGFA 1990) was a fish taken by rod-and-reel off Virginia measuring 819 mm TL (~10.89 kg). Within constraints of the von Bertalanffy equation and length-weight relationship derived for tautog from Virginia waters, we estimate an age for this fish of ~30 yr, which is comparable to the maximum age (34 yr) reported for the species (Cooper 1967).

Weight-at-age estimates for tautog, as a measure of growth, were much more variable than length estimates. This variation is attributed to different stages in ontogenetic development, as well as differences in sex, maturity, and age. Geographic location and associated environmental conditions, such as seasonality (date and time of capture), stomach fullness, disease and parasite loads (Le Cren 1951, Bagenal & Tesch 1978), can also affect weight-at-age estimates. Since these factors contribute significant variation to regression relationships of WT on TL, interpretation of differences in these data between populations must be viewed with caution.

Direct comparisons of our length-weight data with those of Cooper (1967) were not feasible due to sampling differences (Cooper used eviscerated weights of fish). However, in a study of tautog from coastal waters off New York, Briggs (1969) calculated a length-weight relation based on uneviscerated weights of over 3000 fish collected during several seasons (May–November) over a 3 yr period. Although Briggs did not present data for individual sexes, comparisons of data combined for both sexes are still possible (Table 9). From these comparisons, it is evident that the length-weight relationship for tautog from Virginia waters is similar to that estimated for tautog from off New York.

Table 9

Comparison of estimated length-weight relationships between *Tautoga onitis* collected in Virginia (uneviscerated weights, sexes combined; Log W (g)= −4.632+2.979 Log L; n=687) and New York (from Briggs 1969; uneviscerated weights, sexes combined; Log W (oz) = −5.992+2.916 Log L; n=3156).

	Estimated weight (g)	
Length (mm)	New York	Virginia
150	76.5	70.9
200	119.1	112.2
250	334.4	324.7
300	567.0	558.9
350	890.2	884.7
400	1215.4	1316.8
450	1854.1	1870.3
500	2520.3	2560.0
550	3328.3	3400.5
600	4289.4	4406.7
650	4941.4	5096.1

Reproduction and growth

Maximum GSI values calculated in the present study indicate that spawning commences in late April and continues to early June for tautog taken at inshore sites in Virginia. Finding fish in spawning condition in Virginia in late April is somewhat earlier than reported previously for tautog from more northern inshore areas, and undoubtedly reflects the warmer temperatures in coastal waters of Virginia in early spring. Based on laboratory (Olla et al. 1980) and field observations (Chenoweth 1963, Olla et al. 1974, Eklund & Targett 1990, this study) of ripe fish, spawning in tautog generally commences when water temperatures reach 11° C or above. In Massachusetts, tautog spawn from mid-May to early August (Stolgitis 1970), while peak spawning was reported to occur from late May to early June in tautog collected within shallow waters of Narragansett Bay, Rhode Island (Chenoweth 1963). Near Long Island, tautog eggs have been collected in the plankton from May through early September (Perlmutter 1939, Wheatland 1956, Austin 1973); however, the effective spawning season may be somewhat shorter since few larvae were collected when water temperatures exceeded 21.0° C (Austin 1973).

Highest GSI values for tautog from Virginia occurred over a longer seasonal period than reported for tautog collected inside Narragansett Bay (Chenoweth 1963). We attribute this to the fact that we collected fish over a broad range of sites spread over a much wider geographic area, including many deepwater offshore stations. On hardbottom areas 22–37 km offshore of Maryland and northern Virginia, Eklund & Targett (1990) noted significantly higher GSI values for female tautog (24–50 cm TL) from May through the beginning of August, with spawning taking place during summer (May–July). This time schedule is similar to what we observed in tautog collected at offshore habitats in southern Virginia, and, as was pointed out by Eklund and Targett, this seasonality also corresponds with the occurrence of tautog eggs and yolksac larvae in Mid-Atlantic Bight plankton samples (Colton et al. 1979).

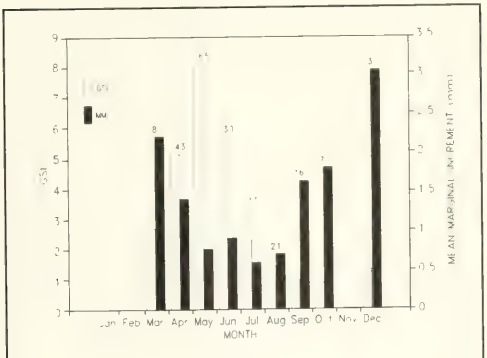

Figure 11

Relationship demonstrating co-occurrence of time of annulus formation (mean marginal increment, MMI) and peak spawning season (gonadosomatic index, GSI) for *Tautoga onitis* from coastal waters of Virginia.

Annulus formation in tautog collected in Virginia occurs in May or June commensurate with gonadal maturation (Fig. 11). Formation of an annulus on the opercle concomitant with spawning was noted also by Cooper (1967) for tautog from Rhode Island. Decline in physiological condition during gonadal development, presumably representing disruption in somatic growth, was observed in tautog by Chenoweth (1963). Such disruption in somatic growth could contribute to the slow-growth phase observed on opercles during this time. However, annulus formation occurs in sexually immature fish during this same time, indicating that inherent physiological factors other than those associated with spawning also influence annulus formation in these fish.

Annulus formation in tautog collected in Rhode Island occurred in late or middle May at the start of the spawning season (Cooper 1967). In Virginia, we observed that annuli formed over a longer time-period (May–July). Warmer water temperatures earlier in spring in Virginia may cause smaller fish to form annuli slightly earlier than larger fish. This growth pattern would agree with observations that younger and smaller fish are more active than larger fish at lower water temperatures (Olla et al. 1974, 1980). Also, since these smaller fish do not usually participate in spawning activities, all growth during spring would be reflected as increases in somatic rather than gonadal growth.

Variation in the estimate of time of annulus formation may have resulted from analyzing data independent of year of collection. Interannual differences in environmental conditions would be expected when these data are combined. Also, we sampled tautog from various geographically separated inshore and offshore locations, and small-scale variations in time of annulus formation may be expected in fish collected from these diverse areas. One other source of variation could result from annulus formation during the spawning period. Since spawning commences earlier and is apparently more protracted for fish in southern areas of the species range, the period for annulus formation would also be extended in tautog occurring in Virginia compared with those occurring further north.

Growth and sexual strategy

The present study, and previous ones conducted in more northern waters (Chenoweth 1963, Cooper 1967, Stolgitis 1970, Briggs 1977), found that male tautog mature by age-3 and females by age-4. Similar age-at-maturation for tautog from different portions of the species range for the present population of tautog living in Virginia's coastal waters, and that reported by Cooper 25 years ago (1967) for tautog from Narragansett Bay, may reflect demographics of populations that have not sustained intensive exploitation. It would be valuable to compare age-growth data for the present-day population of tautog residing in Narragansett Bay with historical data in Cooper (1967) to test this hypothesis.

It is unknown what percentage of tautog in a population mature precociously, under what environmental or social situations, or even if smaller fish are sexually active and reproduce successfully. In May 1985, the second author collected a 180 mm TL, age-2 gravid female north of the confluence of the Taunton River and Mount Hope Bay, Massachusetts. In the present study, no sexually mature females smaller than 230 mm TL or younger than age-3 were found. We note, though, that our data are limited for age-2 fish, especially for fish of this age-group during their second summer and fall. Olla & Samet (1977) also reported collecting sexually mature tautog "which were of a much smaller size and younger age [no sizes or ages reported] than has previously been reported" from coastal waters of New York and northern New Jersey. It is interesting to note that precocious individuals have only recently been reported, and these were tautog occurring in northern waters where sport and localized commercial fisheries have operated historically since the 1800s (Goode 1884) and have undoubtedly intensified since that time. Earlier maturation is a common compensatory response in fish populations subjected to intensive exploitation (Goodyear 1980) and may explain the appearance of precocious individuals in tautog populations inhabiting northern portions of the species range where exploitation has occurred for a longer time.

Sex ratios for tautog divided into 10 cm length-groups were found to deviate significantly from a 1:1 ratio in the larger size-classes, with larger (and older) size-classes of tautog being comprised predominantly of males. Based on a smaller sample size, Eklund and Targett (1990) also reported a sex ratio (0.86:1) skewed in favor of males. Small sample size in their study, however, precluded breakdown of sex ratios over the size range studied. Among other factors, skewed sex ratios in larger (and older) fish may be attributed to differential growth and longevity of males or slowing of growth (measured as TL) with age in females, or possibly as a result of sex reversals. Faster growth coupled with greater longevity for male tautog found in Virginia's coastal waters may reflect the higher energetic costs of reproduction and subsequent earlier senescence and differential mortality for females, as suggested by Cooper (1967). Larger size may also be selected for in males. Observations of courtship and spawning reveal that a size-related male dominance hierarchy is one reproductive mode (group spawning without a dominance hierarchy is the other) occurring in tautog with dominant males exhibiting strong territoriality and performing a protracted courtship with females, culminating in pair-spawning (Olla & Samet 1977). In reproductive strategies involving pair-spawning, territoriality, and dominance social hierarchies, size selection for large males would be advantageous. Such strong size and sexual selection is known in other labrids, including bluehead wrasse *Thalassoma bifasciatum* (Warner et al. 1975), California sheepshead *Semicossyphus pulcher* (Warner 1975), cunner *Tautogolabrus adspersus* (Johansen 1925, Pottle & Green 1979a,b), and others (Warner & Robertson 1978), where females primarily select larger (older) males as spawning partners.

Although diandric male phases are prevalent in both tropical and temperate labrids (Robertson & Choat 1974, Warner & Robertson 1978, Dipper & Pullin 1979), diandric male tautog were not reported in earlier studies (Chenoweth 1963, Cooper 1967). Olla & Samet (1977), following Cooper (1967), noted in their study on spawning behavior that "tautog were easily identifiable with respect to their gender by the sexually dimorphic mandible, which is more pronounced in males." However, in that same paper, unpublished data of Olla & Bejda noted the occurrence of sexually-mature young tautog of both sexes, without any sexual dimorphism. Olla & Samet (1977) suggested that mandibular dimorphism in tautog may develop ontogenetically, becoming apparent only in older, larger fish. In contrast, we found wide overlap (up to ~50 cm TL) in body size between the two male forms, rendering it unlikely that age alone controls development of secondary male characteristics in tautog.

Olla & Samet (1977) also discussed the possibility that younger, mature fish may represent a different sexual stage than that of older fish. They pointed out that nothing was known of behavior or gonadal development of these young fish, and that it was even remotely possible that tautog might be hermaphroditic.

Since two spawning strategies have been observed in male tautog (Olla et al. 1977, 1981), it is possible that diandric males are those that utilize different reproductive strategies. Since non-dimorphic males have coloration patterns reminiscent of females, they may increase spawning opportunities through sneak or in-

terference spawning during activities of territorial males. Reproductive behavior of individual male tautog is flexible and influenced by both size and sexual composition of the population. For example, in some situations with co-dominant males, or when males greatly outnumbered females, group spawning occurred even among dimorphic males that in previous experiments exhibited strong territoriality and more typically attempted only exclusive pair-spawning with females (Olla et al. 1981). Diandric males, each with different reproductive behaviors, have been reported for hermaphroditic labrids (Robertson & Choat 1974, Warner 1975, Warner & Robertson 1978, Dipper & Pullin 1979, Pottle & Green 1979a) and scarids (Warner & Downs 1977, Robertson & Warner 1978). However, diandric males not resulting from sexual inversions, but with different reproductive strategies, have also been reported (Pottle & Green 1979a,b) in cunner *Tautogolabrus adspersus*, another temperate species of wrasse co-occurring throughout most of the geographic range of the tautog.

Plasticity of male reproductive behavior, presence of diandric males in the population, and skewed size and sex-ratios indicate that reproduction in tautog is more complex than recognized previously. Many of these same characteristics are paralleled in protogynous hermaphroditic labrids. In fact, protogynous hermaphroditism is one of the more common reproductive strategies utilized by labrids (Roede 1972, Warner & Robertson 1978). Earlier researchers (Chenoweth 1963, Cooper 1967) did not consider that tautog might be hermaphroditic; others (Olla & Samet 1977) recognized such possibilities, but, as yet, no evidence based on histological examination of gonads exists to prove or disprove the occurrence of hermaphroditism in this species. In view of the complex reproductive biologies of other labrids, further study on reproductive biology of tautog is warranted and is currently under investigation.

Growth rates of tautog, other labrids, and reef fishes

Few published age-growth studies on labrids exist, undoubtedly because most are tropical species that have proven difficult to age reliably and few have commercial or recreational value. However, growth rates available for temperate labrids from the eastern and western Atlantic and eastern Pacific indicate slow growth rates and generally extended longevities in these species (Fig. 12), similar to those reported for tautog. It is possible that slow growth and extended longevities are characteristic not only of relatively large-sized temperate labrids, but also may be an inherent feature of growth patterns in large-sized labrids in general.

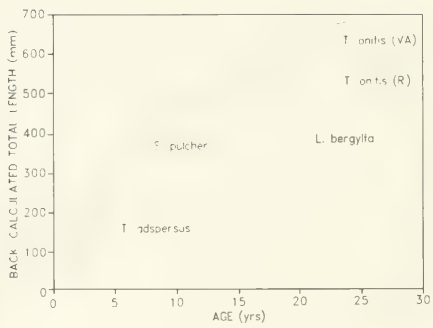

Figure 12

von Bertalanffy growth curves for selected species of temperate and subtropical species of wrasses (Family Labridae). Species represented and information sources for data presented in figure are: *T.*(=*Tautoga*) *onitis*, Rhode Island (Cooper 1965), Virgina, this study; *S.*(=*Semicossyphus*) *pulcher*, Warner 1975; *L.*(=*Labrus*) *bergylta*, Dipper et al. 1977; *T.*(=*Tautogolabrus*) *adspersus*, Serchuk & Cole 1974.

Coefficients derived from the von Bertalanffy growth equation provide insights into ecological strategies, especially in direct comparisons among diverse taxa (Table 10). Manooch (1979) considered fishes such as the bluefish *Pomatomus saltatrix*, Atlantic menhaden *Brevoortia tyrannus*, and king mackerel *Scomberomorus cavalla*, which have relatively high *K*-values (0.23–0.39) indicative of fast growth rates, as the coastal pelagic guild. Species with slower growth rates (*K* usually <0.22) and generally longer lived, on the other hand, were grouped together as the snapper-grouper guild. These fishes represent a wide spectrum of distantly related taxa including temperate labrids, reef-dwelling snappers and groupers, and other demersal fishes such as tilefish *Lopholatilus chamaelonticeps* which inhabits burrows on the continental shelf. Based on categories of growth coefficients adopted by Manooch (1979), we include the tautog in the snapper-grouper guild. This type of comparison, which crosses phylogenetic and demographic lines, suggests similarities in selection patterns for growth rates among species inhabiting areas where spatial resources may be limited.

Conclusions and management considerations

Growing recreational and commercial fisheries for tautog, limited amounts of natural habitat available in

Table 10

Comparison of growth coefficients (K-values) and longevity for selected species of labrids and other coastal fishes (age in years; L_∞ in mm).

Species	Source	Age	L_∞	K
Snowy grouper *Epinephelus niveatus*	Matheson & Huntsman (1984)	17	1255	0.07
Tautog *Tautoga onitis*	this study (males)	25	732	0.09
	this study (females)	22	733	0.09
	Cooper (1965) (males)	27	664	0.09
	(females)	22	506	0.15
Ballan wrasse *Labrus bergylta*	Dipper et al. (1977)	29	405	—
Calif. sheepshead *Semicossyphus pulcher*	Warner (1975)	>20	800	—
Lane snapper *Lutjanus synagris*	Manooch & Mason (1984)	10	501	0.13
Speckled hind *Epinephelus drummondhayi*	Matheson & Huntsman (1984)	15	967	0.13
Mutton snapper *Lutjanus analis*	Mason & Manooch (1985)	14	862	0.15
Tilefish *Lopholatilus chamaeleonticeps*	Turner et al. (1983)	35	960	0.16
Red snapper *Lutjanus campechanus*	Nelson & Manooch (1982)	16	975	0.16
Scamp *Mycteroperca phenax*	Matheson et al. (1986)	21	985	0.17
Cunner *Tautogolabrus adspersus*	Serchuk & Cole (1974)	6	285	0.20
Black sea bass *Centropristis striata*	Wenner et al. (1986)	10	341	0.23
Bluefish *Pomatomus saltatrix*	Wilk (1977)	9	—	0.23
Blue runner *Caranx crysos*	Goodwin & Johnson (1986)	11	412	0.35
King mackerel *Scomberomorus cavalla*	Normura & Rodriques (1967)	14	—	0.35
Atlantic menhaden *Brevoortia tyrannus*	Schaaf & Huntsman (1972)	—	—	0.39

the southern Mid-Atlantic Bight, and the slow growth and reproductive characteristics of this species, suggest a need for a fisheries management plan to maintain the present stocks of tautog in Virginia's coastal waters (and elsewhere). It has been shown that intense fisheries directed at species exhibiting slow growth rates and a habitat-restricted ecology affect populations detrimentally (Manooch & Mason 1984, Matheson & Huntsman 1984, Moore & Labisky 1984, Harris & Grossman 1985, Matheson et al. 1986). Strong habitat preferences (hardbottom with structural relief), slow growth rates, extended longevities (to 25+ yr), and relatively long time to reach sexual maturity (3+ yr), indicate that strategies applied to reef species—the snapper-grouper cohort of Manooch (1979)—may be applicable in managing tautog populations as well.

We suggest as a first step in managing stocks of tautog in Virginia the imposition of size limits on fish taken by recreational as well as commercial fishermen,

since the recreational fishery is the primary harvestor of tautog. A minimum size limit of approximately 300 mm TL (12 in.) is recommended for fish taken by recreational or commercial fisheries to insure that all females have at least one opportunity to spawn before being harvested (Briggs 1977). Imposing a 12 in. size limit for tautog should also insure the maintenance of a quality recreational fishery. Currently, a 12 in. minimum size limit is required for tautog taken by recreational and commercial fishermen in Rhode Island, Massachusetts, and Connecticut waters.

To maximize any management plan for this species, it is also critical that the reproductive biology of tautog be well understood. Directed fishing pressure, disruptive to size or sex ratios by the selective removal of dominant pair-spawning males (usually larger individuals), could affect reproductive success in localized populations. Musick & Mercer (1977) concluded that heavy fishing pressure on black sea bass *Centropristes striata* may impact reproduction through changes in sex ratios in the population.

Tautog populations in Virginia and elsewhere can also be enhanced by continued development of artificial reefs (Feigenbaum & Blair 1986). Reef development is especially important in Virginia since suitable, naturally-occurring substrate appears to be limited both in size and occurrence. Placement of artificial structures over wide geographic areas also disperses fishing pressure, since competition for fishing space on presently-available isolated wrecks can at times be intense.

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Early growth, behavior, and otolith development of the winter flounder *Pleuronectes americanus*

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Abstract. – Studies were performed to determine effects of environment and physiology on the formation of daily increments in winter flounder otoliths. Otoliths from embryonic to 1-yr-old laboratory-raised winter flounder *Pleuronectes americanus* and young-of-year wild-caught specimens were examined, and growth patterns were determined from photographs taken on light and scanning electron microscopes. Behavioral observations were made from hatching through metamorphosis.

Daily growth increments of otoliths from larval winter flounder were enumerated, and a growth curve was derived describing the first 2 months of life. Growth was best described by a Gompertz-type curve. The relationship between sagitta size and fish length was exponential for larvae, but linear during the remainder of the first year. Sagittae were compared with fish length for both wild and laboratory-reared juveniles and exhibited the same relationship for each. The change in relationship between sagitta size and fish length coincided with changes in dimensional growth of the fish.

During metamorphosis, swimming and feeding modes changed from tail-propelled, upright swimming and frequent sudden feeding lunges in larvae, to bottom-resting and creeping accompanied by infrequent feeding gulps in juveniles. This change reflected the transfer from pelagic to benthic habitat and anatomical transformation to asymmetrical form. In general, juveniles maintained lower activity levels than did larvae. Behavioral and anatomical changes are summarized.

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Many aspects of fish development are reflected in otolith structure. Short- and long-term changes in growth rate may be caused by either environmental fluctuations or life history changes (e.g., metamorphosis, spawning), and these events may also be incorporated into the otolith record of sagittae. Hyaline bands have been used for decades to estimate age. Daily growth increments have also been discovered in fish otoliths (Pannella 1971, 1974) and are proving a powerful tool to study larval population dynamics.

One daily growth increment includes both a calcium-rich aragonite layer in a protein-poor matrix (the "incremental zone") and a poorly calcified protein-rich matrix layer (the "discontinuous zone") (Watabe et al. 1982). Increments are entrained in response to a 24 h light/dark cycle (Taubert & Coble 1977, Tanaka et al. 1981, Radtke & Dean 1982) as well as influenced by other cues (Campana & Neilson 1982, Campana 1984a,b). As a result of the daily cycle in calcium deposition, otoliths often reflect fish age, irrespective of growth, although this has not always been found to be the case (Geffen 1982, Campana 1983, Jones 1984). Differences in width and other features of daily growth increments have been correlated to life-history transitions, changes in environmental conditions such as temperature and ration size, and physiological factors (for review see Campana & Neilson 1985, Jones 1986).

Flounders have a particularly complex first year because, not only their habitat, but also much of their body form and behavior changes drastically at metamorphosis (35–56 d after hatching). Hatching as symmetrical larvae that feed planktonically, they begin to frequent the bottom as their dorsoventral dimension increases, the notocord tip bends, and the adult-shaped caudal fin develops (Klein-MacPhee 1978). Finally, the fish spends less time swimming in the water column and becomes benthic. This occurs as one eye migrates across the dorsum to the opposite side of the head and the juvenile flounder orients at a 90° angle to its previous alignment. Otoliths do not change their position in the head during this transformation (Platt 1973, Policansky 1982), so the sagittae end up lying one over the other. Evidence of the fish's orientational change may be reflected in the otolith depositional pattern.

Furthermore, physiological changes as well as the change in food source might also register on the otolith.

This study is the first in a continuing sequence of investigations on the effects of environment and physiology on the formation of subannual increments in winter flounder otoliths. Relationships between behavioral and anatomical changes were defined and correlated with baseline data on daily growth increments. Growth rates of both wild and laboratory-reared larvae were determined. Increment counts and morphological changes from known-age laboratory-reared fish were compared with those of wild fish to establish anatomical markers in the otolith during the first year.

Materials and methods

Acquisition of eggs and larval rearing

Adults caught in Narragansett Bay served as gamete sources. Eggs fertilized in the laboratory were acquired from the National Marine Fisheries Service (NMFS) and Environmental Protection Agency (EPA) laboratories at Narragansett, Rhode Island during February and March 1981. Larvae hatched 15 March 1981 (termed the Mar 15 group) were reared in static trays using methods of Klein-MacPhee et al. (1980). The light cycle was maintained at 11:13 (light/dark). Light intensity in the growth trays varied between 256 and 1777 lux. A separate 114 L tank was maintained for behavioral observations. Light intensity in this tank was 847–4780 lux. Salinity range was 32–33 ‰, temperature was kept at 5–10°C (±1°C) without diel variation until July, when temperature was allowed to roughly follow seasonal patterns (Fig. 1). Larvae were fed once daily unicellular green algae *Tetraselmis souscii* and rotifers *Brachionus sp.*, beginning at 3–5 d before yolksac absorption began. Rotifer concentrations of at least 1/mL were maintained, although concentrations ranged to over 20/mL. When larvae were 40 d old, newly-hatched brine shrimp were added to maintain prey concentrations of 1/mL. After several months, fish were fed frozen brine shrimp with the addition of chopped mussels at irregular intervals.

Heavy mortalities (>90%) reduced larval populations such that only 30 fish survived through metamorphosis (40–60 d posthatch). Of the metamorphosed fish, 11 lived 1 yr and then were killed for otolith examination. Due to physiological effects induced by natural mortality, only otoliths from sacrificed fish were examined.

Sampling

Initially, 10 fish per day selected at random were removed and preserved in 95% ethanol. After hatching,

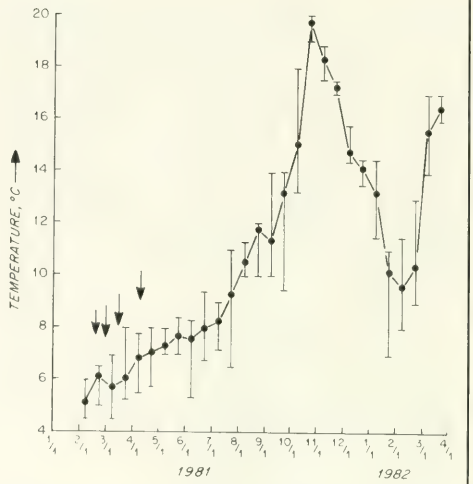

Figure 1

Water temperatures showing mean and range of bimonthly temperatures. Arrows represent hatch-group dates (day of 50% hatch) of winter flounder *Pleuronectes americanus*.

fish were sampled at 1–6 d intervals until metamorphosis. In an effort to conserve the 30 fish surviving metamorphosis, additional samples of laboratory-reared larvae in 95% ethanol were provided for ageing by the NMFS Narragansett Laboratory (hereafter referred to as the LR hatch group). These samples were of larvae 0–55 d old and were reared using the same methods as the Mar 15 hatch group.

Standard length measurements were obtained from preserved fish. To check for shrinkage in body length, larvae were measured before and after 1 week's preservation and percent shrinkage determined.

Collections

Wild young-of-the-year (YOY) winter flounder were collected throughout summer 1981 using beach seines from estuaries along Cape Cod. Otoliths were dissected from these specimens.

Otolith preparation and analyses

Body lengths of preserved larvae were measured on glass slides. In larvae (hatch to ~30 d), sagittae could not be distinguished from the asterisci or lapilli; therefore all otolith pairs were removed and aged. In fish

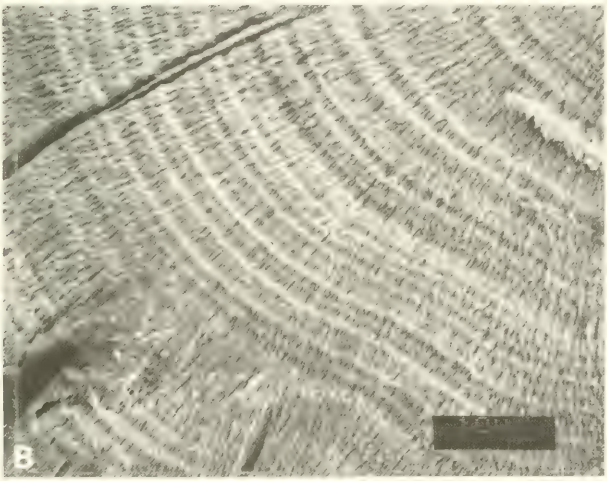

Figure 2
Light microscope **(A)** and SEM **(B)** photographs of winter flounder *Pleuronectes americanus* otoliths showing similarity of detail visible in both. Scale bars represent 10 μ.

30 d and older, sagittae were measured and used for increment counts.

Otoliths were measured to the nearest micron (under a compound microscope) along the longest axis through the central core and along the axis perpendicular to that dimension using an optical micrometer at 200–1000× (depending on otolith size). Most increment counts were done on photographs at 1000×. All increments visible in at least two places on an otolith were counted. Varying the focus changed the resolution of increments; therefore the maximum number of increments seen in a series of pictures taken at slightly-varying focal planes was counted. Two or three separate counts by two age-readers were averaged. If the two readers disagreed by more than two increments or the photographs were considered unclear, that otolith set was not used in daily growth-increment calculations. Increments formed prior to yolksac absorption were either absent or difficult to resolve and were not included in the total count. Based on the work of Radtke & Scherer (1982), a correction factor of 10 was added to the number of observed increments in order to establish each larva's estimated age in days from hatch.

For scanning electron microscopy (SEM) viewing, some of the larger (600–840 μ along the largest dimension) sagittae were prepared according to the methods in Radtke & Dean (1982). Light microscope pictures of an otolith were compared with SEM photographs of the same specimen (Fig. 2) and counts were found to be comparable.

Behavioral observations

Larval behavior was observed from hatching through metamor-

phosis to correlate behavior with physiological (as registered in otolith development) and morphological changes. Observations of the larvae were made in holding tanks throughout the period they were reared. Individual larvae were also observed in small containers under low magnification to verify anatomical changes as well as details of small movements.

On the 48th day after hatching, individuals were moved into an observation tank to facilitate observation. An undergravel filter bed was placed in the refrigerated observation tank to minimize disturbance resulting from maintenance procedures. Temperature, diets, and light-cycle conditions were the same as those for separate tray-reared larvae. Light intensity was higher in the observation tank than in trays because overhead lights were supplemented with tank lights. Fish were observed for 10 min periods twice daily, at 10 a.m. and 4 p.m. One fish chosen at random was followed as long as it could be seen; if it moved out of sight, another individual was selected for the remainder of the observation period. Behaviors recorded included swimming (duration, vertical and horizontal direction, body orientation in relation to the bottom, and fin usage); feeding, both before and after adding food (frequency, location, sequence of body motions, success); resting (duration, location, body position); and interactions between individuals. Observations were terminated several weeks after fish had metamorphosed and behavior patterns had stabilized (i.e., assumed a typical adult sedentary behavior pattern).

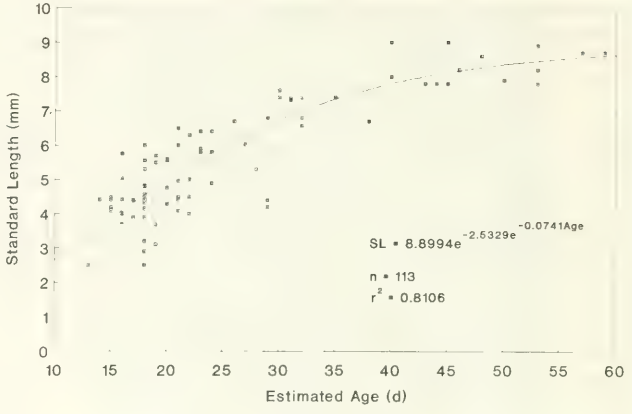

Figure 3

Gompertz growth curve and equation fitted to plot of standard length and estimated age in days (no. of otolith increments + 10) for 113 larval winter flounder *Pleuronectes americanus*.

Results and discussion

Larval growth rates

From analysis of 113 preserved larval winter flounder ranging from 2.5 to 9.0 mmSL, growth was best described by a Gompertz-type curve (Fig. 3). Previous uses of the Gompertz growth curve and methodology for fitting the curve are described in Pennington (1979) and Bolz & Lough (1988). The variance was stabilized by using the natural log form of the growth equation, and parameters were derived by nonlinear estimation techniques resulting in the relationship:

$$\ln(L) = -0.3469+2.5329(1-e^{-0.0741R}),\ r^2=0.8106, \quad (1)$$

where L = standard length in mm, and R = estimated age (increments +10) in days.

The predicted length of 2.66 mm at yolksac absorption compares favorably with that found by Radtke & Scherer (1982) for wild larvae (2.5 mm). The asymptotic length of 8.9 mm probably delineates mean length at metamorphosis and falls within the range (7–13 mm) given by Fahay (1983). The average growth rate (from Eq. 1) for the period under study was 0.31 mm/d, which is slightly less than that observed in the 1982 study using preserved lengths by Radtke & Scherer (0.38 mm/d).

Shrinkage

Little shrinkage was observed for larvae 4–35 d old as has been reported by other researchers (Radtke & Waiwood 1980, Theilacker 1980). Fresh lengths were 2.8–5.0 mm; preserved lengths, 2.5–5.0 mm (n=28) with average shrinkage of 4.2% (SE=0.6). For 91–112 d old flounder, fresh lengths were 5.9–13.8 mm; preserved, 5.8–13.6 mm (n=19) with average shrinkage of 8.6% (SE=0.9). Radtke & Scherer (1982) found no shrinkage in small larvae (<4.7 mm) and only minimal shrinkage (4%) in older fish. Though we observed slightly larger shrinkage than Radtke & Scherer (1982), the growth rates during the 55 d agree roughly with larval flounder growth rates found in their study.

Figure 4
(A) Otoliths taken from winter flounder *Pleuronectes americanus* embryo 13 d after spawning, showing primordial granules in center. **(B)** Rings in otolith taken from embryo 16 d after spawning. Magnification 1000×.

Otolith development

Pre-hatch formation All three pairs of otoliths were present in embryos as early as 13 d after spawning. Premordial granules of material were evident at this time, clumped together in the otolith core (Fig. 4A). The periphery of the otolith forms a rather irregular sphere. Up to four growth rings could be seen on some embryonic otoliths (Fig. 4B). Similar formations have been found on embryonic otoliths of several other species (Taubert & Coble 1977, Brothers & McFarland 1981, Radtke & Dean 1982, Geffen 1983, Brothers 1984), but their periodicity or significance has not yet been determined.

Shape change at metamorphosis At the time of eye migration (40–50 d posthatch), the sagittae of winter flounder underwent a profound change in shape. Clumps of what seemed to be amorphous calcareous material accumulated at the otolith periphery. These accessory growth centers developed irregularly, sometimes appearing two or three on an otolith, often forming at 90° intervals around the circumference of the previously round otolith (Fig. 5A). Similar observations have been made in other Pleuronectids (Brothers 1984, Campana 1984c).

It is significant that accessory growth centers were found only on otoliths of flounders during and after metamorphosis. Larvae with symmetrically-placed eyes did not show these irregular formations on their sagittae, even as late as 73 and 76 d posthatch (Fig. 5B). A photograph of a non-metamorphosing 73 d-old larval otolith without accessory growth centers is compared with that of the typical otolith from a metamorphosing individual in Figure 5. The appearance of asymmetrical formations on sagittae of metamorphosing flounders coincides with the change from vertical to horizontal orientation (i.e., dorsal-side uppermost to right-side uppermost) which accompanies the shift to an asymmetrical form and a benthic habitat. Thereafter, accretion again seems to proceed by increments which coincide with age in days, but which continue an asymmetrical deposition until the adult shape is stabilized. If the formation of accessory growth centers is found to occur at the time of metamorphosis in other flounder species (Brothers 1984, Campana 1984c), this may prove useful in marking the point of habitat change within the otolith record. It is possible that accurate otolith counts could then begin with the juvenile stage rather than the earlier, less easily prepared, and counted larval otoliths.

Fish length/otolith length relationship during the first year The relationship between sagitta size (larg-

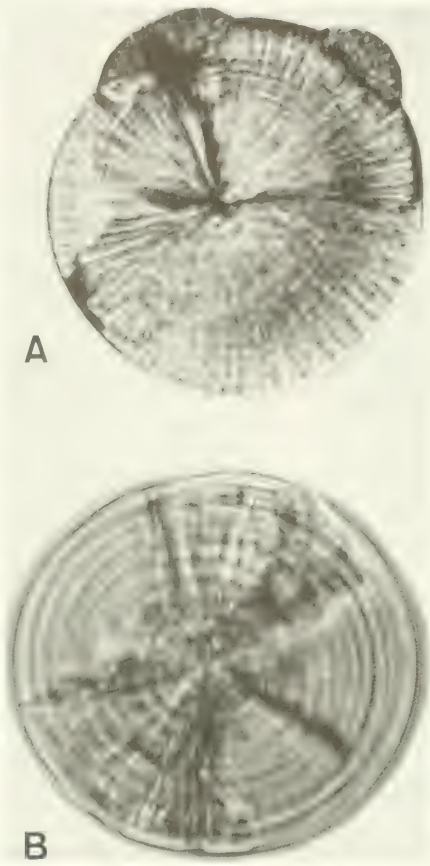

Figure 5

(A) Accessory growth centers on sagitta of metamorphosing winter flounder *Pleuronectes americanus*. **(B)** Symmetrical otolith from 73 d-old winter flounder that had not yet undergone metamorphosis, showing continuing lack of accessory growth centers.

est dimension) and fish length was nonlinear for premetamorphic larvae raised under laboratory conditions (Fig. 6). The best fit equation was exponential,

$$Y = 7.8e^{(0.03x)} \quad (r^2=0.87),$$

where x is standard length and Y is otolith length. Because larger larvae had an average shrinkage of 8.6% as compared with 4.2% for smaller larvae, the parameter estimates in the above equation may not be bias-free. By the end of the first year, however, the relationship was linear (Fig. 7). Covariate analysis indicated that the regression lines for laboratory-reared and wild YOY winter flounders were not significantly different, so data pairs were pooled. The resulting regression line for YOY flounders (about 3 mo or older) using the same variables as above was

$$Y = 0.10+0.29x \quad (r^2=0.95).$$

Both linear and allometric relationships between otolith size and larval fish length have been reported in the literature (Taubert & Coble 1977, Brothers & McFarland 1981, Methot 1981, Radtke & Dean 1981). Although this relationship has been reported for starry flounder (Campana 1984c), it has not been previously reported for larval winter flounder. It is not surprising, however, that otolith growth exceeds growth in body length. Addition to body depth is enhanced as the body form alters towards the adult shape. This feature may compensate for the decline in growth in length at this time (Pearcy 1962, Laurence 1975). Investigating the relationships between length, depth, otolith dimension, otolith mass, and fish mass may in future studies elucidate the relationship between larval flounder somatic growth and otolith growth.

Wild vs. laboratory-reared fish Otoliths from wild juvenile samples showed the same diameter/fish length relationship as otoliths from our laboratory-reared fish. Otoliths from wild fish exhibited a more regular and somewhat sharper depositional pattern of increments. Therefore, these were used more frequently for SEM analysis. The superior clarity and regularity of otolith incremental patterns from wild fish over laboratory-reared fish have been discussed in the literature (Blaxter 1975, Uchiyama & Struhsaker 1981, Radtke & Dean 1982, Radtke & Scherer 1982) and is discussed in detail by Campana & Neilson (1985).

Early larvae: Hatch to 40 d Under a temperature regime of 5–7°C, larvae hatched 14–18 d after being spawned. Hatching was accompanied by intermittent writhing and vibrating motions of the embryos. Hatchlings sank to the tray bottom when not in motion.

Swimming began immediately after hatching. Larvae swam with rapid lateral tail-whips and could control direction. All swam away from disturbances caused by a pipette tip. Swimming became stronger and more sustained over the first 10 d posthatch. On the third day after hatching, a series of brief (1–8 s) upward swims, followed by a 20 s to 1 min passive period resulting in head-down sinkings, were first noted. This intermittent swimming behavior may be adaptive in

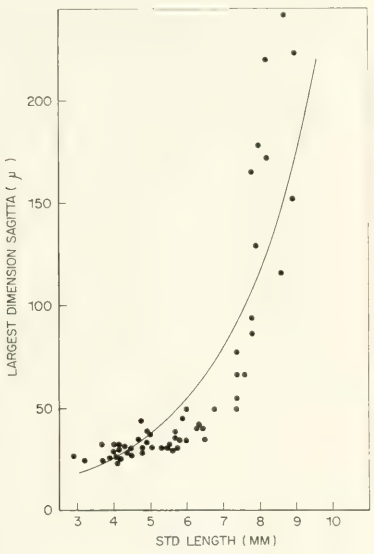

Figure 6

Exponential relationship between sagitta size and standard fish length of winter flounder *Pleuronectes americanus*. $Y=7.8e^{0.3x}$, $r^2=0.87$. Curve represents all points to 94 d posthatch for Feb. 27 hatch data only.

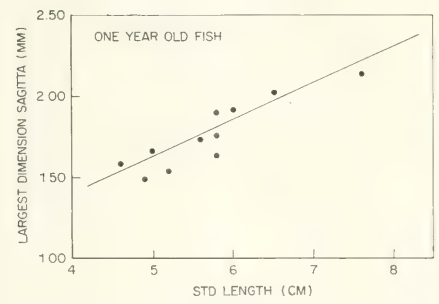

Figure 7

Regression of standard fish length on sagittae size for pooled young-of-the-year winter flounder *Pleuronectes americanus* (3 mo or older). Pooled data include both laboratory-reared and wild collected data ($n=28$). $Y=0.10+0.29X$, $r^2=0.95$.

protecting young larvae from extensive transport by surface currents (Sullivan 1915, Pearcy 1962). Sullivan reported that swimming appeared to be periodically inhibited by a factor other than fatigue. By 7 d, larvae swam for 3–10 s followed by a 2–10 s passive period. After about 25–30 d, swimming was constant during the day except when interrupted by feeding behaviors.

For the first 10 d posthatch, swimming larvae were concentrated at the surface; after about 20 d, larvae were dispersed throughout the water column. There were noticeable aggregations of larvae at tank corners and along sides, but no schooling behavior was observed. Swimming larvae avoided bright microscope lights.

Lunging—defined as a sudden, rapid thrusting motion of the body which propels the larva less than a centimeter forward but which is faster and more abrupt than swimming activity—was observed as early as 5–7 d posthatch (depending on hatch group), before the mouth was completely formed. Once the mouth parts had formed (at the time of yolksac absorption), lunges included rapid and wide jaw gape and snap. Incidence of lunging increased from less than once a minute initially to once every 10 s or more frequently by 40 d posthatch. Systematic observations of lunges began at day 48 (Fig. 8). Prey items were not always visible but were seen often enough that these movements were assumed to be feeding lunges. No lunges were observed after day 72 coincident with metamorphosis.

A sigmoid coiling of the body, called an "S motion" here, often preceded the lunge. This motion could be slow or fast, and when rapid often included a single side lunge as the body was pulled backwards and the head whipped from one side of the "S" to the other. The rapid "S" was first observed 5–9 d posthatch, while the slow one was not noted until 30–50 d posthatch. Larval feeding by such an "S strike" motion has been described for other species in the literature (Rosenthal & Hempel 1970, Hunter 1972). The slow "S motion" we observed in older larvae is speculated to be related to the greater accuracy of striking prey facilitated by experience.

Successful feeding, defined by observation of at least one food particle in the gut of sampled larvae, began at 9–14 d posthatch, at or just after yolksac absorption (8–12 d posthatch). However, growth has been reported to slow or stop for several days after absorption of the yolksac (Cetta & Capuzzo 1982).

Passive, nonswimming yolksac larvae sank in a head-down position in the water column until they hit bottom or abruptly resumed swimming towards the surface. When on the tray bottom, they lay on either side, or on top, of their yolksac. As swimming duration increased, time on the tray bottoms decreased until, after 20 d (when the yolksac was no longer present), few were seen on the bottom. Passive, nonswimming behavior in the water column was, however, observed past 20 d. After yolksac absorption (~12 d posthatch)

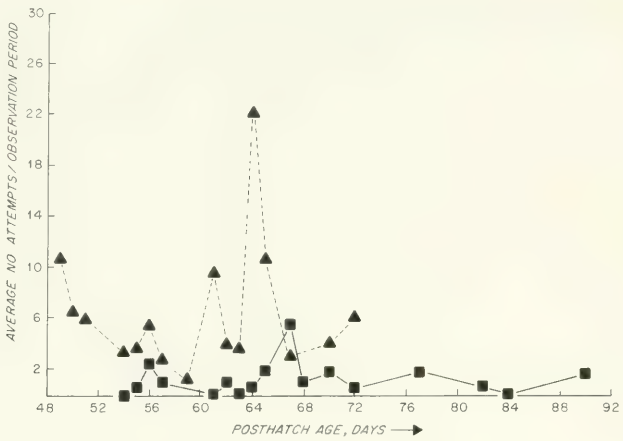

Figure 8

Incidence of winter flounder *Pleuronectes americanus* feeding behaviors, average number of lunges in water column (▲) versus average number of gulps on bottom (■). Note change in feeding behavior from frequent pre-metamorphic lunging to less-frequent post-metamorphic gulping. No lunging was observed after day 72.

the larvae began to maintain their bodies in a horizontal position as they sank, instead of sinking in the vertical, passive, nonswimming position.

Behavior at metamorphosis: 40–60 d posthatch Eighteen fish were placed in the observation tank on day 48 so that their behavior could be more closely monitored. The following account is based on those observations.

By 40–50 d posthatch, larval body form began to change. The body widened dorsoventrally, pigment developed (especially over the head, jaw, gut, and fins), and the end of the notocord began to bend as the adult caudal fin formed. These physical changes, described more fully by other researchers (Sullivan 1915, Breder 1922), took place concurrently with the behavioral changes described below.

The most obvious behavioral changes were seen in swimming and resting patterns. Larvae up to 50–60 d posthatch swam upright using the tail-whipping motion. The body was positioned with dorsal fin uppermost, and the eye had not yet migrated. Beginning at 48 d, occasional interruption of swimming was noted as fish drifted in the water column, usually maintaining an upright posture but not moving fins or tail. At 55 d, the first observation of canted swimming was recorded. Fish rose off the bottom in response to disturbances and swam at about a 60° angle to the side, then sank to the bottom again. Only larvae whose eye was in the process of migration (asymmetrical placement) were seen to swim at an angle in this way, and only infrequently were these individuals observed swimming in the water column.

Fish with obviously widened bodies and adult-shaped tails began the transition to bottom habitat just prior to eye migration (~40–50 d posthatch). Eight fish were observed lying on the bottom by 42 d posthatch, either on their ventral or left sides. Apparently, some of these individuals returned to larval swimming patterns, since only three were not in the water column on day 48. From day 42 until the last record of fish seen in the water column (day 72), swimming fish were seen to sink to the bottom, either head-down or horizontally oriented, and usually rested on their left side for varying periods before swimming up from the sand, again with an upright larval swimming posture (Fig. 9). Other observations of left-side resting have been reported as early as 10–12 d posthatch (Sullivan 1915).

Eye migration was difficult to observe precisely. It has been reported (Sullivan 1915) to occur over an interval of several days, and we observed that it appeared to occur shortly after establishment of the developing larva on the tank bottom. Once eye migration was completed, fish were never seen to swim upright. However, they occasionally entered the water column lying horizontally on the left side, slowly rippling their dorsal and ventral fins rhythmically.

Newly metamorphosed fish were relatively inactive, lying on the bottom for 10 min or more at a time, occasionally moving their eyes. Activity and metabolic levels have been reported elsewhere to decrease dramatically at this point in flounder development (Blaxter & Staines 1971, Laurence 1977). The first slow bottom swimming with rippling dorsal and ventral fins or "creeping" activity was noted on day 55 during metamorphosis.

Bottom-resting fish also "darted" at intervals, swimming in a rapid burst propelled by tail beats. A dart appeared somewhat like a long lunge in its suddenness and in its generation by caudal body motions rather than fin motions. Darting was also observed in unmetamorphosed fish in the water column as an infrequent reaction to a disturbance. The earliest obser-

vation of darting in bottom-resting fish occurred on day 54. Darting persisted as a sporadic activity in metamorphosed juveniles.

Metamorphosing fish fed in the water column as did unmetamorphosed larvae. Feeding behavior was observed throughout the daylight period. Other researchers have noted the strictly diurnal feeding behavior of young winter flounder (Laurence 1977).

Newly metamorphosed fish resting on the bottom were observed "gulping" on day 55. Gulping was a relatively inactive feeding behavior, with the jaw gape and snap found in the lunge but not accompanied by other body movements. Postmetamorphic juveniles increased the incidence of gulps with age, sometimes combining a short creep and a gulp but often showing no other sign of active feeding. After metamorphosis is complete, increased feeding efficiency, coupled with decreased metabolic requirements, results in comparatively low energy expenditures associated with feeding behavior (Blaxter & Staines 1971, Laurence 1977).

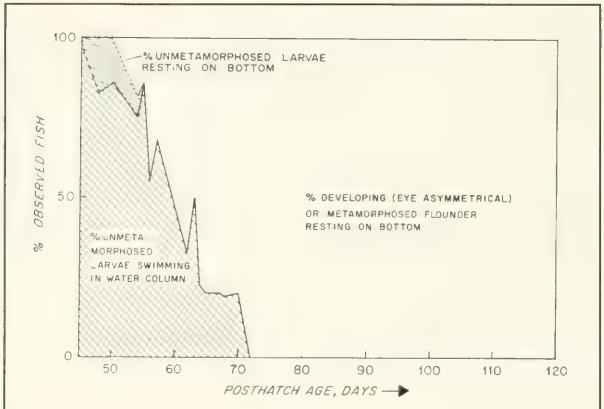

Figure 9

Swimming vs. resting behavior of pre-metamorphosed versus developing (eye asymmetrical) or post-metamorphosed winter flounder *Pleuronectes americanus*. 3–18 fish were observed in each 10 min period. Average number observed/period was 7.

Conclusions

In this study, larval winter flounder otoliths were found to reflect internal and external changes indirectly. Daily growth increments did not begin immediately after hatching, although some individuals exhibited otolith rings at hatch. Daily growth increments were not visible beginning at yolksac absorption. Rather, increments were visible beginning at a point midway between yolksac absorption and the beginning of metamorphosis. These increments may have reflected internal changes presaging metamorphosis, although such changes are not yet externally evident. The period during which these increments appeared was also the period during which swimming behavior during the day became constant, except when it was interrupted by feeding behavior. Shortly after this time-period, the slow "S motion" was first exhibited as a feeding behavior, possibly correlated with experience and better feeding efficiency.

Metamorphosis resulted in obvious behavioral changes as well as anatomical ones. Swimming began with an upright position in which the tail was whipped back and forth to provide propulsion. Larvae then went through a period of canted swimming before settling into swimming on their sides using a rippling of their fins for most propulsion. Horizontal swimming with rippling fins was associated with the change to a more benthic existence. The horizontal swimming style occurred less frequently than the earlier upright one, which was consistent with a decrease in overall activity levels. Individuals spent increasing amounts of time resting on the bottom as metamorphosis progressed. At this time, slow bottom "creeping" was first exhibited along with the relatively inactive "gulping" feeding behavior.

The external changes in body shape at metamorphosis corresponded with internal change in sagittae shape. Otoliths from metamorphosed juveniles were found to exhibit accessory growth centers. Sagittae from older fish that had not yet undergone metamorphosis did not exhibit these centers and consequently were still spherical.

The connections between fish growth, behavioral ecology, and physiology are still not well understood. There is clearly a connection between behavior and physiology, although the causality of change in morphology, growth, and behavior is still unclear. This study attempted to correlate some of the behavioral and anatomical changes.

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Abstract.—The larval development of three roughy species complexes, *Paratrachichthys* sp., *Aulotrachichthys* sp., and *Optivus* sp., is described and illustrated using larvae collected from Tasmanian and New South Wales waters. Larvae were identified using meristic and morphological characters and are characterized by differences in head and dermal spination, size at caudal flexion, and size and pigmentation of the pelvic fins. Head spination is well developed in *Aulotrachichthys*, and weak in *Optivus* and *Paratrachichthys*. Dermal spination is well developed in postflexion *Aulotrachichthys* and flexion *Optivus*, but absent in *Paratrachichthys*. Development of a luminous organ and anterior migration of the anus occur much earlier in *Aulotrachichthys* than *Paratrachichthys* and are notably absent in *Optivus*. The use of these larval characters in trachichthyid systematics, and the possible reasons for the absence in our samples of larvae attributable to orange roughy *Hoplostethus atlanticus*, are discussed.

Larval development of three roughy species complexes (Pisces: Trachichthyidae) from southern Australian waters, with comments on the occurrence of orange roughy *Hoplostethus atlanticus*

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The family Trachichthyidae (order Beryciformes) consists of some 31 species, of which at least 15 occur in southern temperate waters of Australia (May & Maxwell 1986). Seven genera are known from Australian waters: *Hoplostethus, Paratrachichthys, Aulotrachichthys, Optivus, Gephyroberyx, Trachichthys*, and *Sorosichthys*. The various species inhabit depths from nearsurface to greater than 1200 m, with most occurring in depths greater than 200 m. There is considerable confusion regarding the taxonomy of the group, and a number of the species occurring in Australian waters are undescribed. The genus *Hoplostethus* comprises at least three Australian species—*H. intermedius*, *H. latus*, and orange roughy *H. atlanticus* (May & Maxwell 1986)—which supports a recently developed fishery. *Paratrachichthys* is represented in Australian waters by the sandpaper fish, *Paratrachichthys* sp., an undescribed species that is closely related to, and has only recently been distinguished from, the New Zealand endemic *P. trailli* (M. Gomon, Mus. Victoria, Melbourne, pers. commun., Nov 1990). Specimens have been recorded from New South Wales, Victoria, South Australia, Tasmania, and southern Western Australian waters (May & Maxwell 1986).

Aulotrachichthys and *Optivus* each contain two closely-related undescribed Australian species (M. Gomon, pers. commun.). *Aulotrachichthys* sp.1 occurs in shallow waters of South Australia, whereas *Aulotrachichthys* sp.2 occurs in deeper water off the east coast (May & Maxwell 1986). Similarly, *Optivus* has both eastern and western Australian representatives: *Optivus* sp.1 along the east coast as far north as southern Queensland, and *Optivus* sp.2 off southern Western Australia (May & Maxwell 1986). The remaining three genera are monotypic, represented by *Gephyroberyx darwini*, *Trachichthys australis*, and *Sorosichthys anannassa*.

Little is known about the ecology or early life history of trachichthyids, and there is nothing in the literature on the early life history of Aus-

tralian species. Parr (1933) and Johnson (1970) described 19 mm and 21.5 mm juvenile *Korsogaster*, respectively, a genus subsequently synonymized with *Hoplostethus* by Woods & Sonoda (1973). Crossland (1981) illustrated a trachichthyid larva, possibly *Optivus elongatus*, from northeastern New Zealand. Robertson (1975) described an egg tentatively ascribed to *Paratrachichthys trailli*. Kotlyar (1984) described juveniles of four species of *Hoplostethus* (including a 36 mm *H. atlanticus*), the smallest of his specimens being a 15 mm *H. melanopterus*. Okiyama (1988) figured and briefly described single specimens of an unidentified *Hoplostethus* (10.7 mm), *Gephyroberyx japonicus* (11.0 mm), and *Paratrachichthys prosthemius* (27.5 mm).

Comparatively little is known of trachichthyid larval characters; however, common characters include precocious pelvic fin development, heavy pigment, a stocky body form approaching the shape of adults (in larger larvae), a myomere count of 26–30, and the presence of minute spines over the body surface (Keene & Tighe 1984, and references therein).

Recent commercial interest in the orange roughy *Hoplostethus atlanticus* has emphasized the need for information on the early life history of this species. As yet, despite considerable effort in ichthyoplankton sampling, no *H. atlanticus* larvae have been reported from Australian waters. The current study describes the larval development of three trachichthyid species complexes—*Paratrachichthys* sp., *Aulotrachichthys* sp., and *Optivus* sp.—in specimens obtained from plankton samples collected primarily in Tasmanian and New South Wales coastal waters from 1984 to 1986. These descriptions are presented in order to further define larval characters that may be of use in trachichthyid systematics and future identification of other trachichthyid larvae, including *H. atlanticus*.

Materials and methods

Specimens were largely obtained from ichthyoplankton samples collected in 1984–86 by the CSIRO Division of Fisheries, Hobart, Tasmania, as part of a study aimed at documenting the distribution and abundance of larval fishes in Tasmanian coastal and neritic waters. Details of sampling locations and protocol are provided by Thresher et al. (1989). Larvae were obtained from oblique tows to a depth of 200 m (bottom depth permitting) at a series of stations covering shelf and slope waters, using a 1 m diameter ring net (500 µ mesh). Additional material was obtained from samples collected with identical gear in New South Wales shelf and slope waters by A. Miskiewicz (Water Board, Environ. Proj. Group, PO Box A53, Sydney South, 2000).

Larval samples were fixed in either 10% formalin buffered with sodium tetraborate, or 95% ethanol. Morphometric analysis and illustrations were based on formalin-fixed specimens of *Paratrachichthys* and *Optivus*. However, only ethanol-fixed material was available for *Aulotrachichthys*. No allowance was made for shrinkage or distortion in preservative.

Larvae were examined using a Wild M5 dissecting microscope, and all drawings were made with the aid of a camera lucida. Larvae were identified using existing literature (Keene & Tighe 1984, Okiyama 1988) by comparison with juvenile and adult features of identified species, and by the establishment of developmental series. Comparisons with similar larvae (e.g., zeids) were made with material from the CSIRO samples.

All unspecified body lengths refer to notochord length in preflexion and flexion larvae, and to standard length in postflexion larvae and juveniles. We define **snout to anal-fin length** as the horizontal distance from the tip of the snout to the anterior origin of the anal fin or anal-fin anlagen. **Body depth at anus** is the vertical distance between body margins through the center of the anal opening. **Body depth at pectoral** is equivalent to 'body depth' of Leis & Rennis (1983). Other definitions, such as body shape, follow Leis and Trnski (1989). Nomenclature of head spination follows that of Moser & Ahlstrom (1978). Larval measurements were made using an ocular micrometer. Juveniles were measured with vernier calipers.

Results

During 18 months of sampling, 119 *Paratrachichthys*, 147 *Optivus*, and 25 *Aulotrachichthys* larvae were collected. The distribution of larvae is detailed in Figure 1. No larvae that could be attributed to *Hoplostethus* were collected. A representative series of each species was deposited in the ISR Munro Fish Collection (CSIRO, Hobart, Tasmania). Reference numbers: *Optivus*, CSIRO L179-184; *Paratrachichthys*, CSIRO L185-190; *Aulotrachichthys*, CSIRO L191-196.

Identification

In larger specimens of two of the series, the anus is located between the pelvic fins. Only three trachichthyid genera have this character: *Paratrachichthys*, *Aulotrachichthys*, and *Sorosichthys* (May & Maxwell 1986). *Sorosichthys* is separated easily on the basis of a pelvic count of I,5, compared with the I,6 of the other two genera (Table 1). The only character reported in the literature to distinguish adults of *Aulotrachichthys* from *Paratrachichthys* is the presence in

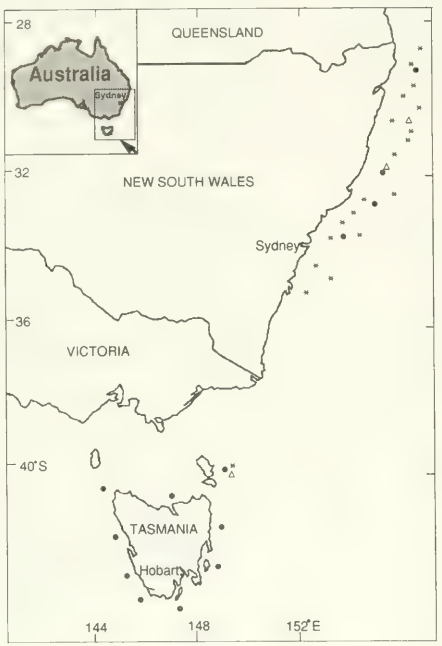

Figure 1

Distribution of trachichthyid larvae sampled in southeast Australian waters. (●) *Paratrachichthys* sp., (*) *Optivus* sp., (△) *Aulotrachichthys* sp.

the former of striated silvery tissue on the bases of the pectoral fin, on the isthmus beneath the gill cover, and in a narrow strip along the ventral edge of the body (May & Maxwell 1986). However, examination of juvenile and adult specimens also reveals a difference in anal fin-ray counts: *Paratrachichthys* with a count of III,10 and *Aulotrachichthys* with III,8. Both series had a pelvic count of I,6. An anal count of III,8 and striated pectoral tissue occurred in the largest specimen of only one series; on that basis, we assign the series with the largest specimen to *Aulotrachichthys* and the other to *Paratrachichthys*. We were unable to determine whether or not the *Aulotrachichthys* and *Optivus* series represented more than one species. *Optivus* larvae were distinguished on the basis of a dorsal count of IV,11, an anal count of III,9, and the position of the anus, which remains static, immediately anterior to the anal fin.

Table 1

Meristic characters of trachichthyid genera present in southern Australian waters.

	D	A	P1	P2	Vertebrae
Paratrachichthys	V,13	III,10	12–14	I,6	27–29
Aulotrachichthys	V,13	III,8	12–14	I,6	27–29
Optivus	IV,11	III,9	10–12	I,6	27–29
Hoplostethus	V-VIII,12–18	III,9–11	12–20	I,6	25–30
Gephyroberyx	VIII,13–14	III,11	14	I,6	26–27
Sorosichthys	IX-X,8–9	II,8	13	I,5	Unknown
Trachichthys	IV,10–14	III,9–11	11–14	I,6	27

Larval development

Paratrachichthys sp. (Fig. 2)

Morphology Head length is about equal to body depth at pectoral until flexion, after which body depth increases to approximately 50% of body length (Table 2). The mouth is large, reaching to approximately the center of the eye in our smallest specimen (3.2 mm) and beyond the eye in larvae greater than 4.5 mm (Fig. 2A-C). The body depth at anus increases markedly during flexion, associated with the anterior migration of the anus during this period. The gas bladder is inflated and prominent in all specimens. There are 27–29 myomeres.

Initially the gut is straight and tube like. It quickly thickens, coils, and becomes triangular by approximately 5.0 mm. The anus begins to migrate anteriorly by 6.5 mm and is in the adult location (between the pelvics) by 7.8 mm (Fig. 2E). The light organ surrounding the anus first appears in 5.4 mm larvae as an unpigmented, thickened ring. By 6.1 mm the light organ is lightly pigmented; by 6.9 mm the organ is heavily pigmented and rugose. Notochord flexion commences at about 5.9 mm and is complete by 7.6 mm.

Fin development Development of the pelvics is precocious. Slight swellings on either side of the gut are present in our smallest specimen (3.2 mm). Distinct buds are present by 3.9 mm. The pelvics develop rapidly, having a full complement of 7 elements by 5.6 mm, and reaching up to 34% body length by 7.6 mm. Anlagen of both dorsal and anal fins are present by 4.3 mm. The anlagen first appear as hyaline zones within the fin folds, connected to the body by a series of filamentous extensions inserted at each myoseptum (Fig. 2B). Bases of the anal and dorsal fins are present by 4.7 mm, and posterior incipi-

Table 2

Body proportions of larvae and juveniles of *Paratrachichthys* sp. (expressed as mean proportions of body length with standard deviations in parentheses). Specimens between dashed lines were undergoing notochord flexion. Characters lacking standard deviation are based on one individual only. *n*=number of individuals.

Size range (mm)	*n*	Snout to anal fin	Preanal length	Body depth (at pectoral)	Body depth (at anus)	Head length	Eye diameter	Pelvic fin length
3.32	1	–	0.62	0.19	0.10	0.22	0.13	–
3.90	1	–	0.68	0.22	0.09	0.28	0.12	0.06
4.01–4.50	5	–	0.59(0.03)	0.26(0.02)	0.12(0.01)	0.29(0.01)	0.12(0.01)	0.11(0.04)
4.51–5.00	7	0.63(0.02)	0.62(0.02)	0.28(0.03)	0.14(0.01)	0.30(0.01)	0.14(0.01)	0.18(0.02)
5.01–5.50	8	0.63(0.02)	0.62(0.02)	0.34(0.02)	0.19(0.04)	0.31(0.02)	0.14(0.01)	0.25(0.03)
5.51–6.00	3	0.61(0.02)	0.57(0.01)	0.35(0.02)	0.26(0.04)	0.33(0.02)	0.15(0.01)	0.27(0.02)
6.01–6.50	2	0.60(0.05)	0.54(0.07)	0.38(0.03)	0.29(0.05)	0.33(0.01)	0.15(0.01)	0.29(0.01)
6.95	1	0.70	0.55	0.43	0.39	0.35	0.14	0.30
7.60	1	0.74	0.43	0.53	0.43	0.41	0.17	0.34
10.00	1	0.71	0.48	0.42	0.42	0.34	0.17	0.26
35.80	1	0.58	0.38	0.38	0.38	0.34	0.14	0.18
39.70	1	0.60	0.37	0.39	0.39	0.36	0.12	0.18

ent rays first appear above these bases by 5.4 mm. Incipient rays appear in the pectoral fin shortly thereafter (5.5 mm). Ossification of dorsal, anal, pelvic, and pectoral fins occurs during flexion, with full complements in all fins present by 7.8 mm.

Spination *Paratrachichthys* larvae have only weakly developed head spination. A low supraocular ridge is present at 3.3 mm, developing 1–2 spines by 3.9 mm (Fig. 2A). The number of supraocular spines increases to 2–3 by 4.0 mm, reaching a maximum of 5–6 just prior to flexion. During flexion, the supraocular spines disappear.

The single opercular spine is present by 6.9 mm and is retained in the adult. Similarly, single preopercular and posttemporal spines are present by 8.7 mm and are retained. Cranial ridges are present by 5.4 mm; however, even by 10.0 mm these have not yet become denticulate as they are in juveniles and adults.

Scalation Juvenile and adult *Paratrachichthys* have small, adherent, ctenoid scales covering the body and a series of strong ventral scutes between the anus and the anal fin (Woods & Sonoda 1973). Our largest larva (10.0 mm) has no sign of scalation and lacks the minute dermal spines of other trachichthyid genera, although a weak fleshy ridge develops along the ventral midline between the anus and the anal fin by 7.6 mm, probably a precursor to the characteristic ventral scutes of juveniles and adults. The 39.7 mm juvenile examined was, in effect, a minature adult having completed scalation, including the ventral scutes.

Pigmentation *Paratrachichthys* larvae are moderately to heavily pigmented (with the exception of the last 2–8 myomeres, including the notochord tip) throughout the entire larval period. Pigment tends to be concentrated over the dorsal and ventral surfaces of the body and the dorsal surface of the gut. Otherwise, there are few useful distinguishing features based on patterns of pigmentation.

The pelvic fins are heavily pigmented by 4.2 mm and remain so in our largest postflexion larva (10.0 mm). Some variation was introduced by the obviously faded pigment of certain specimens, the result being a series of heavily-pigmented and a series of moderately- to lightly-pigmented individuals. Because the major pigment concentrations, morphology, and meristic information were otherwise identical for the two series, it is unlikely that variations in the intensity of pigmentation indicate the presence of more than one species.

Aulotrachichthys sp. (Fig. 3)

Morphology Head length is about equal to body depth at the pectoral fin until flexion, after which body depth increases to 50% body length (Table 3). The mouth is moderately large, reaching to the posterior margin of the eye in our smallest specimen (2.8 mm), falling to just short of the margin in our largest specimen (7.9 mm). The body depth at the anus increases markedly prior to flexion as the anus migrates anteriorly. The gas bladder is inflated and prominent in all speci-

mens. There are 27–29 myomeres.

The gut is a convoluted tube in our smallest specimen (2.8 mm). It quickly thickens, coils, and becomes triangular by 4.4 mm. The anus begins to migrate by 3.9 mm and is in the adult location (between the pelvic fins) by 4.9 mm (Fig. 3C,D). A light organ that surrounds the anus first appears in 3.6 mm larvae and is well developed, rugose in appearance, and heavily pigmented by 4.4 mm. Ventral striated tissue, characteristic of adults, is present in the 7.9 mm specimen.

Insufficient specimens were available to fully document flexion; however, flexion was just about to commence in a 4.9 mm specimen, was well underway in a 5.7 mm specimen, and had been completed in a 7.9 mm specimen.

Fin development Development of the pelvic fins is precocious. Even our smallest specimen has a full pelvic complement of 7 elements (although ossification is not completed until 4.4 mm). The pelvic fins are large, up to 35% body length at 4.9 mm, and reach beyond the anal-fin origin in all specimens. The limited number of specimens precluded documenting initial dorsal- and anal-fin anlagen development; however, the separation from the body of the posteriormost anal base in our 4.1 mm specimen suggests a finfold development similar to *Paratrachichthys*. Both dorsal and anal bases are present by 3.9–4.1 mm, and incipient rays appear above these bases by 4.4 mm. Incipient rays appear in the pectoral fin shortly thereafter (4.9 mm). Ossification of the dorsal, anal, and pectoral fins commences in flexion-stage larvae, with a full complement in all fins present by 7.9 mm.

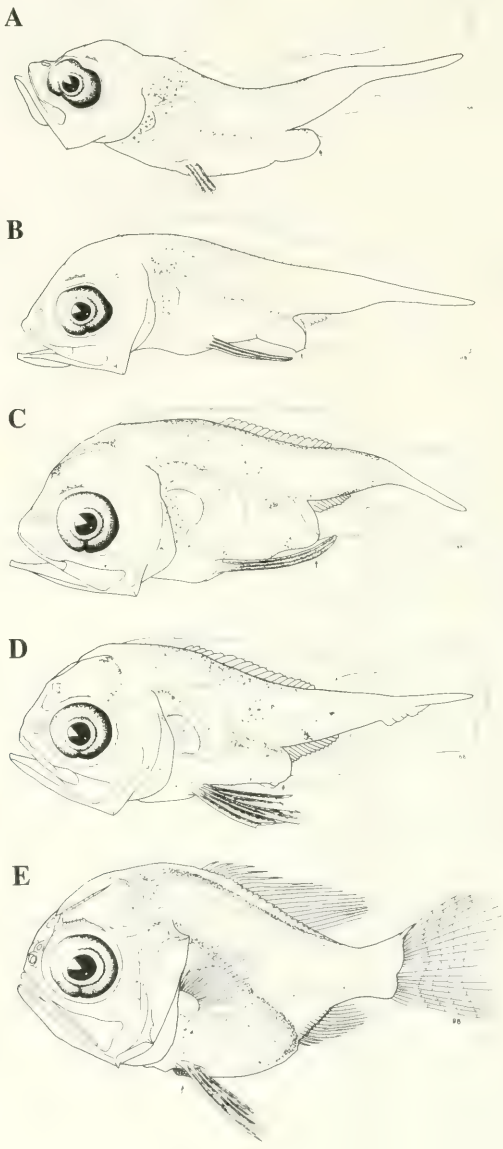

Figure 2
Development stages of *Paratrachichthys* sp.: **(A)** 3.9 mm, **(B)** 4.3 mm, **(C)** 4.7 mm, **(D)** 5.5 mm, **(E)** 7.8 mm. Arrows indicate location of anus.

Table 3

Body proportions of larvae of *Aulotrachichthys* sp. (expressed as mean proportions of body length with standard deviations in parentheses). Specimens between dashed lines were undergoing notochord flexion. Characters lacking standard deviation are based on one individual only. *n*=number of individuals.

Size range (mm)	*n*	Snout to anal fin	Preanal length	Body depth (at pectoral)	Body depth (at anus)	Head length	Eye diameter	Pelvic fin length
2.51–3.00	5	–	0.59(0.05)	0.25(0.03)	0.14(0.02)	0.24(0.02)	0.11(0.01)	0.23(0.01)
3.01–3.50	3	–	0.63(0.01)	0.25(0.01)	0.14(0.01)	0.27(0.02)	0.13(0.01)	0.27(0.03)
3.51–4.00	3	–	0.60(0.03)	0.34(0.03)	0.18(0.04)	0.31(0.02)	0.13(0.01)	0.33(0.03)
4.01–4.50	2	0.62(0.01)	0.54(0.01)	0.34(0.02)	0.22(0.02)	0.31(0.01)	0.13(0.01)	0.31(0.00)
4.91	1	0.59	0.38	0.39	0.37	0.34	0.13	0.35
5.66	1	0.64	0.30	0.35	0.51	0.30	0.16	0.28
7.85	1	0.72	0.44	0.50	0.50	0.43	0.17	0.31

Spination *Aulotrachichthys* larvae have well-developed head spination. Our smallest specimen has a low supraocular ridge with a single spine. The number of supraocular spines increases to 3–4 by 4.4 mm (Fig. 3C); they become quite robust and reach a maximum number of 8–9 during flexion. Generally, the posterior group of these spines are the largest and are recurved. Preopercular spines are present by 4.4 mm, with an anterior preopercular series added by 4.9 mm. By 5.7 mm, preopercular spination is quite robust, with secondary ridging and branching of the largest spines (particularly at the angle) (Fig 3D). Nuchal, supracleithral, and posttemporal spines, as well as nasal and cranial ridges, are developed prior to 5.7 mm. During flexion a hard bony plate forms in the region of the posttemporal, extending posteriorly to the level of the opercular margin. This plate extends beyond the opercular margin by 7.9 mm, and is retained in the adult. Available specimens are insufficient to determine if this plate results from the fusion of the supracleithral and posttemporal series. During flexion, spines also develop on the dentary and infraorbital. Several cranial and opercular ridges appear at this stage.

A single spine is present immediately posterior to the anus by 4.9 mm. Dermal spines are present on the pelvic bases by 5.7 mm, and by 7.9 mm a cluster of spines is also present immediately anterior to the anus. The 7.9 mm specimen has well developed dermal spination in longitudinal rows over the entire body surface and on the dorsal- and anal-fin bases, although there is no sign of scalation. Additionally, this specimen has a row of strong spines extending posteriorly along the ventral midline from the anus towards the anal fin, probably precursors to the ventral scutes of adults. Fine villiform teeth are present in both jaws.

Pigmentation *Aulotrachichthys* larvae are heavily pigmented (with the exception of the posteriormost 5–6 myomeres, including the notochord tip) throughout the larval period. The pelvic fins are heavily pigmented in the smallest specimen and remain so in the 7.9 mm specimen. *Aulotrachichthys* larvae are more heavily pigmented than *Paratrachichthys*, although, as with *Paratrachichthys*, there are few useful distinguishing characters based on pigment pattern.

Optivus sp. (Fig. 4)

Morphology Body depth increases to a maximum of 49% body length during flexion (Table 4). Body depth at anus increases only slightly compared with *Paratrachichthys* and *Aulotrachichthys*, because the anus position in *Optivus* remains static. Head length increases from 36% body length in preflexion larvae to 44% in juveniles. Eye diameter remains relatively constant. The mouth is moderate to large, reaching to the center of the eye in our smallest specimen (2.5 mm) and beyond the eye in larvae greater than 4.0 mm. The gut, which is initially straight, quickly thickens, coils, and becomes broadly triangular by 3.5 mm. *Optivus* larvae do not develop a light organ. Notochord flexion commences at about 4.0 mm and is complete by 7.1 mm. There are 27–29 myomeres.

Fin development Pelvic fins first appear in larvae of 3.0 mm as slight swellings on either side of the gut,

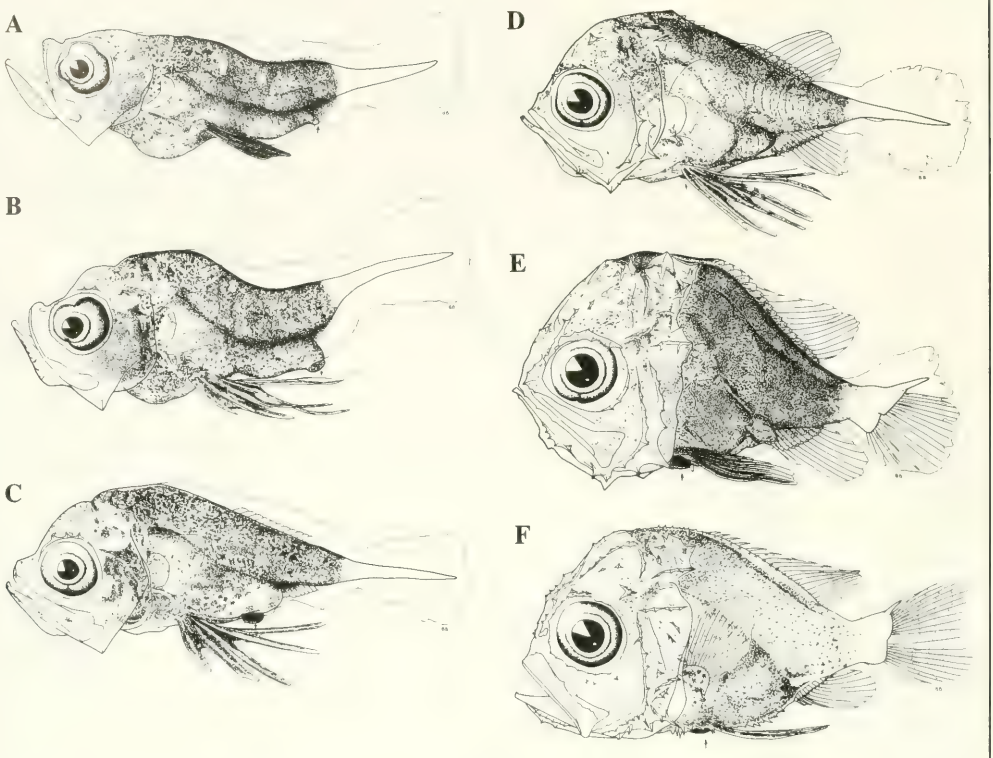

Figure 3
Development stages of *Aulotrachichthys* sp.: **(A)** 2.9 mm, **(B)** 3.4 mm, **(C)** 4.4 mm, **(D)** 4.7 mm, **(E)** 5.7 mm (note: pectoral fin missing), **(F)** 7.9 mm. Arrows indicate location of anus.

and these develop rapidly. Distinct buds are present by 3.2 mm, and the developing fin reaches up to 25% body length by 6.2 mm (Fig. 4A-C). Ossification commences by 5.1 mm, and a full complement of seven elements is present by 8.0 mm. Anlagen of both dorsal and anal fins are present by 2.7 mm and appear as hyaline zones located within the median finfolds, as in *Paratrachichthys*. Bases are first visible in both fins by 3.5 mm, and incipient rays are present by 4.0 mm. Incipient rays appear in the pectoral fin by 4.5 mm. Ossification of the dorsal, anal, and pectoral fins commences in early-flexion-stage larvae, with a full complement in all fins present by 7.1 mm.

Spination Head spination is only weakly developed in preflexion *Optivus* larvae. A low supraocular ridge is present by 2.7 mm, with 4–5 spines developing by 3.4 mm (Fig. 4A). By 4.5 mm, these supraocular spines have disappeared. Cranial ridges are present by 4.7 mm, and a series of spines develops on the preopercular margins by 5.1 mm. The preopercular, opercular, and posttemporal spines characteristic of adults are present by 23.0 mm (Fig. 4E).

Scalation Small dermal spines appear on the body by 4.7 mm and develop in longitudinal rows over the entire body and dorsal- and anal-fin bases by 5.1 mm. By 8.0 mm the base of each single dermal spine has trans-

Table 4

Body proportions of larvae and juveniles of *Optivus* sp. (expressed as mean proportions of body length with standard deviations in parentheses). Specimens between dashed lines were undergoing notochord flexion. Characters lacking standard deviation are based on one individual only. *n*= number of individuals.

Size range (mm)	*n*	Snout to anal fin	Preanal length	Body depth (at pectoral)	Body depth (at anus)	Head length	Eye diameter	Pelvic fin length
2.51–3.00	3	0.66(0.03)	0.68(0.04)	0.34(0.01)	0.18(0.01)	0.36(0.01)	0.13(0.01)	–
3.01–3.50	8	0.66(0.03)	0.66(0.03)	0.38(0.03)	0.20(0.02)	0.35(0.02)	0.14(0.01)	0.05(0.01)
3.51–4.00	9	0.69(0.08)	0.65(0.05)	0.40(0.05)	0.20(0.02)	0.36(0.03)	0.14(0.02)	0.08(0.02)
4.01–4.50	11	0.67(0.04)	0.65(0.04)	0.44(0.05)	0.24(0.04)	0.40(0.03)	0.15(0.02)	0.12(0.02)
4.51–5.00	5	0.69(0.04)	0.67(0.04)	0.45(0.04)	0.26(0.05)	0.40(0.04)	0.15(0.01)	0.14(0.01)
5.01–5.50	3	0.74(0.01)	0.70(0.04)	0.45(0.04)	0.30(0.03)	0.45(0.04)	0.14(0.04)	0.20(0.02)
6.01–6.50	2	0.72(0.03)	0.69(0.06)	0.49(0.01)	0.29(0.02)	0.46(0.01)	0.16(0.02)	0.25(0.02)
7.15	1	0.71	0.70	0.48	0.30	0.43	0.15	0.20
8.00	1	0.72	0.69	0.47	0.31	0.45	0.15	0.20
10.01–10.50	2	0.70(0.07)	0.69(0.08)	0.44(0.02)	0.30(0.01)	0.44(0.01)	0.15(0.01)	0.21(0.03)
15.00	1	0.62	0.60	0.39	0.28	0.36	0.13	0.23
17.40	1	0.63	0.61	0.37	0.28	0.36	0.13	0.19
17.80	1	0.62	0.60	0.38	0.27	0.36	0.13	0.20
18.40	1	0.65	0.64	0.38	0.27	0.35	0.14	0.21
19.60	1	0.63	0.62	0.37	0.27	0.34	0.13	0.18
23.00	1	0.65	0.63	0.37	0.27	0.35	0.12	0.19

formed into a small ctenoid scale (Fig. 5A). Not all scales develop spines at the same stage; by 10.2 mm, scales have 1–3 spines (Fig. 5B). Three spines appear to be present on all scales by 23.0 mm. A row of larger spines appear on the ventral surface between the anus and the pelvic fins by 7.2 mm and form the characteristic ventral scutes of juveniles and adults by 15.0 mm.

Pigmentation Pigmentation in preflexion *Optivus* larvae is moderate and concentrated on the dorsal surface of the gut, as well as the dorsal and ventral surfaces of the trunk. Pigment is absent from the posteriormost 5–6 myomeres (including the notochord tip) as in *Paratrachichthys* and *Aulotrachichthys*. During flexion, the entire body and head become moderately pigmented and the dorsal surface of the gut becomes heavily pigmented. The entire body and head is evenly pigmented in the largest specimen (23.0 mm, Fig 4E). The pelvic fins are moderately pigmented by 4.7 mm; the pigment contracts towards each base during flexion and disappears by 23.0 mm.

Discussion

Considerable confusion exists in the systematics of beryciform fishes at the species level. Current classifications are based almost entirely on adult characters. Keene & Tighe (1984) noted the usefulness of including early-life-history characters in these studies, but the lack of such data at that time for ten of the beryciform families precluded an adequate appraisal. The three genera featured here together share characters common to other described trachichthyid larvae, including moderate to heavy pigment, a moderate to large mouth, a stocky body form, precociously-developing and heavily-pigmented pelvic fins, cranial ridges, opercular spination, and a myomere count of 26–30. Pelvic-fin pigmentation is most pronounced in *Aulotrachichthys* and *Paratrachichthys* and is least developed in *Optivus*. Dermal spination is well developed in *Aulotrachichthys* and *Optivus*, although absent in *Paratrachichthys*. Cranial ridges and opercular spines are present in all of our series; however, *Aulotrachichthys* develops by far the most pronounced head spination of the three and perhaps of any reported trachichthyid larva.

Small trachichthyid larvae can be confused with zeids and some gadoid larvae that also have precocious, heavily-pigmented pelvic fins. However, zeid larvae are more evenly pigmented, have pigment extending into the finfolds in small larvae, generally have a higher myomere count (29–42, Tighe & Keene 1984), and have a more tightly coiled gut with consequently a longer postanal length. The sequence in which fin-ray ele-

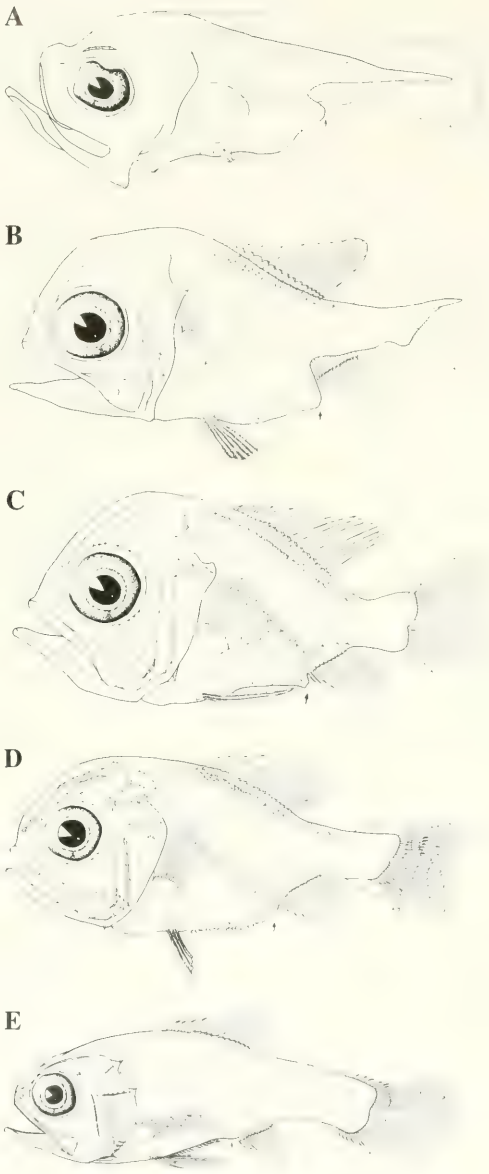

Figure 4

Development stages of *Optivus* sp.: **(A)** 3.4 mm, **(B)** 4.7 mm, **(C)** 5.1 mm, **(D)** 7.2 mm, **(E)** 23.0 mm (note: scale spination not figured). Arrows indicate location of anus.

ments form also distinguishes zeid larvae. In zeid larvae examined during this study, the anteriormost bases and rays were the first dorsal-fin elements to form. In trachichthyids, however, the middle or posterior elements are the first to form. When present, supraocular spination was also a useful feature to distinguish trachichthyids from zeids (zeids examined did not develop supraocular spines until after flexion). Although this may be useful locally, some zeid species (e.g., *Zeus faber*) have supraocular spines at sizes similar to trachichthyid larvae (Sanzo 1931). Larger zeid larvae are easily distinguished from trachichthyid larvae by their longer dorsal- and anal-fin bases, often with elongate anterior rays, a larger mouth, and a rhomboid, laterally-compressed body shape.

Small gadoid larvae with precocious, heavily-pigmented pelvics (e.g., *Gaidropsarus*) differ from trachichthyids in having a higher myomere count (>40), pelvics set higher on the body, and a more slender postanal body form. Larger gadoid larvae are easily distinguished by morphology, fin meristics, and pigment (see Dunn & Matarese 1984, for details).

Hoplostethus species, and in particular orange roughy *H. atlanticus*, are by far the most abundant trachichthyids in Tasmanian waters. Despite extensive sampling throughout the year covering pelagic environments from nearshore to mesopelagic and epipelagic zones (see Thresher et al. 1989, for details), no larvae of the genus *Hoplostethus* have been identified. New Zealand researchers also have been unable to locate *H. atlanticus* larvae (Pankhurst & Conroy 1987), even though spawn-

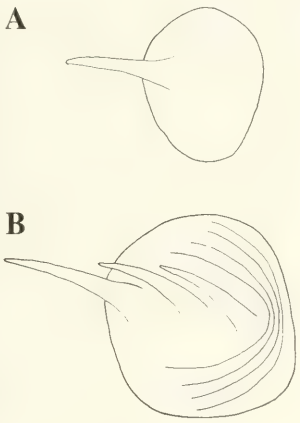

Figure 5
Development of dermal spination on scale of *Optivus* sp.: **(A)** 8.0 mm, **(B)** 10.2 mm.

ing aggregations have been located (Beardsell 1984).

The 26 mm *Hoplostethus atlanticus* specimen, caught in a demersal trawl at 400–950 m off St. Patricks Head, eastern Tasmania (CSIRO H1141), represents the smallest *H. atlanticus* reported to date (Fig. 6). Kotlyar (1984) previously recorded a 36 mm *H. atlanticus* taken by bottom trawl in the Atlantic Ocean at a depth of 965–990 m. The 26 mm juvenile has characters that are common to the other trachichthyids identified, such as a deep body, large mouth, cranial ridges and opercular spination, heavily-pigmented gut and pelvic fins, and distinct anal- and dorsal-ray bases. It is highly likely that such characters are retained in the larvae of *H. atlanticus*, and *Hoplostethus* larvae in general.

Several scenarios may explain why *Hoplostethus atlanticus* larvae have not yet been located.

1 Bimonthly sampling frequency is too coarse to capture larvae during their pelagic stage. Although this cannot be discounted due to the lack of information on larval duration, the likelihood of completely missing all larvae seems low.

2 Larvae occur further off the shelf or slope than sampled (>18 km from the shelf break).

3 Larvae may occur in greater depths than those sampled in 'standard' ichthyoplankton surveys. This may be the most reasonable scenario, and has previously been suggested by Kotlyar (1984) for *Hoplostethus* less than 15–19 mm (based on the capture of three *H. melanopterus* juveniles 15.0–18.2 mm in Isaacs Kid trawls at 1000–1500 m in the Sulu Sea). Larvae may also occur close to the bottom on the continental slope, as supported by the capture of our 26 mm specimen and that by Kotlyar (1984).

Hoplostethus atlanticus adults occur in depths of 500–1200 m (May & Maxwell 1986). Spawning has been confirmed from both the east coast of Tasmania (Lyle et al. 1989) and New South Wales (Williams 1989). *Hoplostethus atlanticus* eggs (2.12–2.45 mm in diameter with a conspicuous orange oil droplet) have been collected in plankton tows above 400 m in Tasmanian (Lyle et al. 1989) and New Zealand waters (Beardsell 1984), and are presumably bouyant. The lack of larvae in surface waters, however, suggests that egg density, the presence of a thermocline, or a combination of both factors may confine eggs and larvae to deep water. Although deep-water plankton sampling is logistically more difficult than shallow-water sampling, such sampling should be carried out if we are to fully understand the early life histories of certain deep-water species.

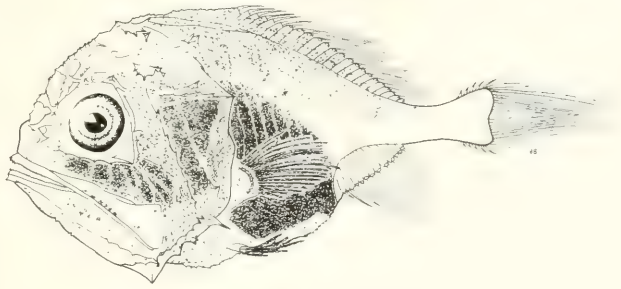

Figure 6
Hoplostethus atlanticus juvenile, 26 mm.

Acknowledgments

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Abstract.—A manned submersible was used in the eastern Gulf of Alaska to observe spatial distributions of Pacific ocean perch *Sebastes alutus* and other *Sebastes* spp., and count rockfish for comparison with bottom-trawl catch rates. Twenty submersible dives were completed in 1988 and 1989 at depths of 188–290 m. Approximately 80% of the 5317 rockfish observed from the submersible were Pacific ocean perch. Most adult Pacific ocean perch were in groups of 2–200 over flat, pebble substrate. Fish within a group were 1–4m apart, usually oriented into the current, and 0–7m above bottom. Most juvenile Pacific ocean perch, and juveniles and adults of other *Sebastes* spp., were associated with rugged habitat (cobble, boulders, pinnacles, and coral). Densities of Pacific ocean perch estimated from bottom-trawl catches were approximately twice those observed from the submersible, indicating that the bridles and otter doors herded fish into the trawl. Bottom-trawl surveys may overestimate Pacific ocean perch abundance because of this possible herding effect and the preference of adult Pacific ocean perch for smooth (trawlable) substrate.

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Distribution and abundance of rockfish determined from a submersible and by bottom trawling

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Pacific ocean perch *Sebastes alutus* is a commercially important rockfish found along the North American coast from southern California to the Bering Sea, and along the Asiatic coast from Cape Navarin to the Kuril Islands (Balsiger et al. 1985). Primarily an offshore species that inhabits the outer continental shelf and upper slope regions, it is caught with bottom trawls at depths of 165–290 m (Hart 1973).

In the Gulf of Alaska, Pacific ocean perch were heavily exploited in the 1960s by the Soviet and Japanese trawl fleets. Foreign catches of rockfish (consisting mainly of Pacific ocean perch) peaked in the Gulf of Alaska in 1965 at 350,000 metric tons (t). By the late 1970s, rockfish catches had declined to less than 10,000 t, and catch-per-unit-effort (CPUE) had decreased by 80% (Balsiger et al. 1985). Domestic trawling replaced foreign trawling in the Gulf of Alaska in the 1980s. Although rockfish stocks remain depressed from overfishing, domestic rockfish catches (mainly Pacific ocean perch) have increased in the Gulf of Alaska from 1000 t in 1985 to 20,000 t in 1990 (Heifetz & Clausen 1990).

Reliable stock assessments are needed for managing depressed stocks of Pacific ocean perch. Current stock assessments, based primarily on catch rates from bottom-trawl surveys, are questionable because (1) the catch efficiency of bottom trawls on Pacific ocean perch is unknown, (2) Pacific ocean perch are not sampled in areas where the habitat is too rugged for bottom trawling, and (3) information is limited on Pacific ocean perch spatial distribution, migration, and off-bottom movement. Leaman & Nagtegaal (1986) noted their dissatisfaction with rockfish bottom-trawl surveys because of wide confidence intervals associated with the biomass estimates, and because alternate assessment techniques indicate that the estimates themselves may be grossly in error. Balsiger et al. (1985) reported that bottom-trawl surveys probably underestimate populations because Pacific ocean perch occupy the water column above the opening of the trawl.

An understanding of both the behavior and habitat of Pacific ocean perch and the catch efficiency of bottom trawls is needed to improve biomass estimates. In this study, a two-man submersible was used for *in situ* observations of rockfish and a bottom trawl to sample rockfish at submersible dive sites. The main objectives were to describe the spatial distribution of rockfish, visually determine their abundance in trawlable and untrawlable habitat, and determine the efficiency of bottom trawls for capturing rockfish. Pacific ocean perch was the target species of this study.

Materials and methods

Study area

This study was conducted in August 1988 and 1989 on the outer continental shelf in the eastern Gulf of Alaska (Fig. 1). Study sites extended over a 300 km range to include a wide range of habitats and population densities of Pacific ocean perch. Dive sites were selected from coordinates of previous trawl and sonar studies: (1) Sites north of lat. 56° N from studies by the Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, in July 1987 and 1988 using bottom trawls, midwater trawls, and sonar to locate high and low densities of rockfish at high-relief (untrawlable) and low-relief (trawlable) sites; and (2) sites south of lat. 56° N from studies by Leaman & Nagtegaal (1986) who used sonar to locate high densities of rockfish at untrawlable sites.

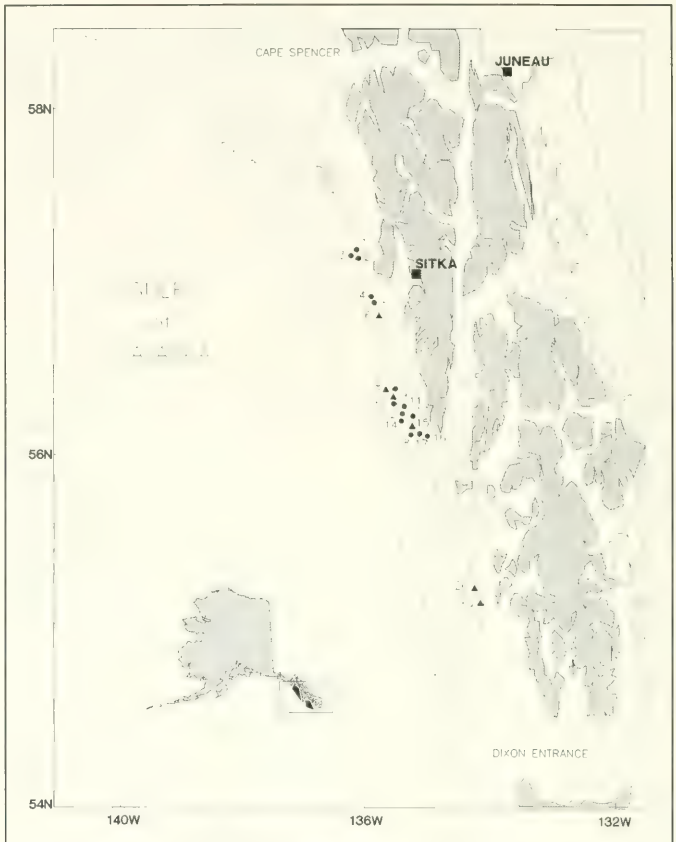

Figure 1

Locations of submersible dive sites in the eastern Gulf of Alaska, 1988 (▲) and 1989 (●).

Submersible

The submersible *Delta* was chartered for all dives. This battery-powered two-man submersible is 4.7 m long, dives to 365 m, and travels 2–6 km/h for 2–4 h. It is equipped with ten 150 W external halogen lights, internal and external video cameras, a 35 mm external camera, magnetic compass, directional gyro compass, underwater telephone, and transponder that allowed tracking of the submersible from the surface vessel *Wm. A. McGaw*.

Submersible transects were charted from the *Wm. A. McGaw*. The surface vessel tracked the submersible and recorded LORAN fixes at the beginning and end of a transect, and every 5–15 min during a transect. In 1988, a transect consisted of a single compass heading followed for 60 min. The transect pattern was changed in 1989 to facilitate trawl comparisons, and consisted of four parallel compass headings followed for 15 min each. The four parallel transects were each separated by 5 min of travel.

A pilot and one of the two observers were aboard the submersible on each dive. The pilot maintained the submersible within 0.5 m of bottom at 3–4 km/h while the observer made observations through a starboard porthole; external cameras were mounted on the starboard side, and the side portholes provided the widest range of view. Observations included rockfish species identification, number, size, grouping behavior, orientation, position relative to the sea bottom, habitat affiliations, and reactions to the submersible. Additional observations included identification and enumeration of other fish species, and estimates of current direction and velocity based on the bending of sea pens and drift of silt. The pilot sat above the observer in a

tower with a panoramic view and assisted in counting fish above the observer's view and in monitoring fish behavior completely around the submersible. All observations were audio- and video-recorded for subsequent analysis and verification. All dives were during daylight between 0600 and 1900 h.

Rockfish densities were derived from the number of fish counted and the seafloor area searched. The seafloor area searched was the distance traveled (1.7–2.2 km/dive) times estimates of the lateral distance from the submersible at which rockfish were visible. Lateral distance estimates varied between 5 and 6 m because of changes in water clarity; illumination was provided entirely by the submersible lights and remained constant. Estimated distances were compared with true distances using three methods: (1) A length of pipe marked at meter intervals was laid on the seafloor on two dives, (2) a hand-held sonar gun provided distance readouts to rock formations on six dives, and (3) the submersible's sonar provided distance readouts to the seafloor during descent and ascent. Estimates of distance were consistently within 1m of true distances. About 10 m was monitored above the submersible: 5–6 m by the observer and an additional 4–5 m by the pilot.

Dive sites were classified as trawlable, marginally trawlable, or untrawlable based on bottom type and extent of relief. Trawlable sites contained pebble substrate interspersed with cobble <0.5 m in diameter on flat bottom; marginally trawlable sites contained pebble substrate interspersed with cobble and boulders of 0.5–5.0 m in diameter on low-relief bottom; untrawlable sites contained mainly bedrock substrate with a variety of rugged habitats including boulders, coral, ledges, rocky outcroppings, and pinnacles on high-relief bottom.

Bottom trawling

Bottom trawling was used in 1989 to identify fish species at submersible dive sites and to derive population densities from catch rates. Trawling was conducted from the NOAA ship RV *Townsend Cromwell*, using a 400-mesh Eastern otter trawl equipped with 1.5×2.1 m doors, each weighing 386 kg. Trawling was during daylight, usually within 4h after completion of a submersible dive. The time between dives and trawls depended on ship's operations, including how long it took to process the catch. The sampling strategy was to trawl at 6.0 km/h, intersecting the four parallel submersible transects at each dive site.

Trawl catches were processed for total number and weight by species. The fork lengths of rockfish were measured to the nearest centimeter. Fish density estimates were derived from the number of fish captured and the seafloor area swept by the net. The seafloor area swept was the distance trawled (0.93–1.35 km/haul) times the horizontal opening of the net (14 m, based on measurements between the wing tips, 12.2–14.3 m for the 400-mesh Eastern otter trawl; NMFS 1990). Measured vertical openings were 1.4–1.8 m.

Data analysis

The off-bottom distance monitored from the submersible was about 10 m, whereas the trawl sampled to about 2 m off bottom. Correlation between the percent composition of fish species observed from the submersible and captured with bottom trawls was determined using correlation analysis (Sokal & Rohlf 1981). Correlations were determined for rockfish, flatfish, shortspine thornyhead *Sebastolobus alascanus*, and walleye pollock *Theragra chalcogramma*.

Correlation analysis also was used to examine the correlation between densities of rockfish observed from the submersible and densities derived from trawl catch rates. Ratio estimates (Cochran 1977) of observed and trawl densities were then used to determine the catch efficiency of bottom trawls for rockfish. For these analyses, Pacific ocean perch, sharpchin rockfish *S. zacentrus*, redstripe rockfish *S. proriger*, and harlequin rockfish *S. variegatus* >25 cm long were categorized as "large"; whereas those ≤25 cm were categorized as "small." Most "large" rockfish observed from the submersible were identified as adult Pacific ocean perch (based on symphyseal knob and body shape), whereas "small" rockfish could not be consistently identified. Rockfish were visually categorized as either large or small from the submersible, whereas trawl-caught fish were measured. Other rockfish species observed from the submersible included redbanded *S. babcocki*, rosethorn *S. helvomaculatus*, dusky *S. ciliatus*, silvergray *S. brevispinis*, yelloweye *S. ruberrimus*, and greenstriped *S. elongatus*. These solitary, demersal rockfish were identified from the submersible by their distinct color patterns, and categorized as "other" rockfish.

Results and discussion

Submersible dives

Six submersible dives were completed in 1988 and fourteen in 1989 at 188–290 m depths. Thirteen of the dive sites were classified as trawlable, three as marginally trawlable, and four as untrawlable. Of the 9278 fish observed from the submersible, 5317 were rockfish (Table 1). Rockfish were the most abundant fish on 11

dives and second in abundance on 9 dives. Of the rockfish, 76% were large, 21% small, and 3% other. Other commonly observed fish were shortspine thornyhead, flatfish, and walleye pollock (Table 1).

Distribution of large rockfish

Large rockfish were solitary or in groups of 2–200 fish. Of the 4020 large rockfish observed, 998 (25%) were solitary and 3022 (75%) were divided about equally among groups of 2–10, 11–50, and 51–200 (Table 2). Although 53% of the rockfish were in groups of more than 10 fish, the number of these groups were few: 56 groups of 11–50 fish and 9 groups of 51–200 fish, compared with 303 groups of 2–10 fish (Table 2). The infrequent occurrence of large groups probably contributes to the high variability of trawl catch rates encountered during rockfish surveys.

Regardless of group size, large rockfish were separated by 1–4 m, were similar in size within each group,

Table 1

Numbers of rockfish and other fish observed at 20 submersible dive sites in the eastern Gulf of Alaska, 1988 and 1989.

Site	Site type*	Distance between sites (km)	Depth (m)	Surveyed area ($10^3 m^2$)	Number of fish					
					Rockfish	Thornyheads	Flatfish	Pollock	Other	Total
1	MT		204–208	13.3	80	96	59	3	34	272
		2.6								
2	MT		204–209	13.8	304	221	7	0	16	548
		3.5								
3	MT		188–211	15.2	151	319	49	1	106	626
		44.1								
4	T		196–198	14.5	104	129	24	48	17	322
		0.6								
5	T		190–193	13.7	124	79	45	47	10	305
		9.3								
6	T		202–207	10.0	42	135	19	3	0	199
		55.2								
7	T		203–207	15.3	198	178	42	9	5	432
		2.8								
8	U		226–290	9.0	44	86	2	0	5	137
		1.7								
9	T		220–227	13.2	47	89	12	0	4	152
		0.7								
10	T		210–213	13.6	83	121	40	0	15	259
		3.2								
11	T		204–210	13.9	376	88	50	35	6	555
		1.1								
12	T		207–210	12.1	234	122	58	53	2	469
		8.2								
13	T		192–192	12.0	1015	37	60	60	10	1182
		3.2								
14	T		195–200	12.3	760	58	53	42	4	917
		8.0								
15	T		213–221	10.5	98	92	20	0	6	216
		24.6								
16	T		197–208	14.8	863	45	40	15	4	967
		2.8								
17	T		192–207	12.9	136	23	96	37	4	296
		4.8								
18	U		192–211	11.8	298	188	10	0	10	506
		128.0								
19	U		201–259	12.0	248	260	12	0	9	529
		9.1								
20	U		195–259	13.2	112	250	13	0	14	389
				Totals	5317	2616	711	353	281	9278

*MT = marginally-trawlable site; T = trawlable site; U = untrawlable site.

Table 2

Numbers of solitary and grouped rockfish and distribution by group size of large and small rockfish observed at 20 submersible dives sites in the eastern Gulf of Alaska, 1988 and 1989.

	Solitary	Grouped							
		2–10		11–50		51–200		Total	
Site	No. fish	No. groups	No. fish	No. groups	No. fish	No. groups	No. fish	No. groups	No. fish
				Large rockfish					
1	38	4	9					4	9
2	71	13	35	2	32			15	67
3	77	15	33					15	33
4	33	7	20					7	20
5	90	9	20					9	20
6	20								
7	71	33	116					33	116
8	11	4	9					4	9
9	18	8	24					8	24
10	57	7	21					7	21
11	75	28	80	1	36	1	160	30	276
12	34	14	57	5	98			19	155
13	172	48	90	17	283	3	300	68	673
14	114	40	131	10	197	2	233	52	561
15	17	10	50	2	27			12	77
16	38	29	93	17	373	3	325	49	791
17	24	12	41	1	41			13	82
18	14	8	21	1	20			9	41
19	10	8	31					8	31
20	14	6	16					6	16
Totals	998	303	897	56	1107	9	1018	368	3022
				Small rockfish					
1	16	3	14					3	14
2	51	3	9	3	69			6	78
3	13	6	17					6	17
4	16	7	30					7	30
5	5	2	5					2	5
6	18	2	4					2	4
7	1	1	3					1	3
8	17	2	7					2	7
9	4								
10	0	1	3					1	3
11	16	3	6					3	6
12	2	1	4	1	35			2	39
13	49	14	58	3	56			17	114
14	26	8	19	2	33			10	52
15	0	1	2					1	2
16	12	1	2	1	18			2	20
17	12	3	18					3	18
18	1	10	40	5	144			15	184
19	50	14	47	1	49	1	60	16	156
20	51	8	29					8	29
Totals	360	90	317	16	404	1	60	107	781

and were usually motionless and facing the current (Fig. 2). Their vertical distribution ranged 0–7 m above bottom. Rockfish in groups of 1–5 rockfish were usually 0–1 m above bottom, whereas rockfish in larger groups were 0–7 m above bottom. No large rockfish were seen above 7 m, either by the observer while ascending, descending, or traveling off the bottom, or by the pilot who searched to 10 m above bottom. This

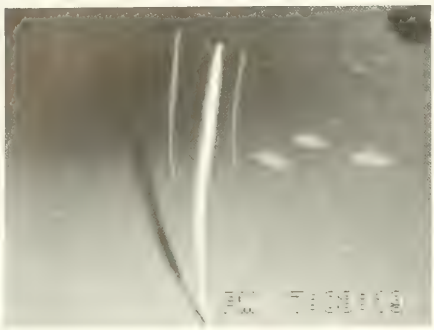

Figure 2

Photograph from the submersible of adult Pacific ocean perch *Sebastes alutus* spaced about 1 m apart and facing into the current. Current direction is indicated by the bend in the sea pens.

observation is supported by results of previous studies that used echosounding equipment to locate off-bottom rockfish, and midwater and bottom trawls to capture fish. In Queen Charlotte Sound, British Columbia in 1976, Pacific ocean perch were the dominant species in bottom-trawl catches, but were not a significant component of midwater-trawl catches targeting off-bottom fish echosignals (Gunderson & Nelson 1977). In the Gulf of Alaska in 1987 and 1988, Pacific ocean perch were not captured in midwater-trawl hauls that targeted fish echosignals 10–30 m off bottom, but Pacific ocean perch were abundant in bottom-trawl hauls (NMFS Auke Bay Lab., Juneau, unpubl. cruise reps. JC 87-04 and JC 88-03).

Table 3

Densities (no./1000 m^2) of large and small rockfish at trawlable (T), marginally-trawlable (MT), and untrawlable (U) sites observed from a submersible.

	Large rockfish			Small rockfish		
Site	T	MT	U	T	MT	U
1		3.5			2.3	
2		10.0			9.3	
3		7.2			2.0	
4	3.6			3.2		
5	8.0			0.7		
6	2.0			2.2		
7	12.2			0.3		
8			2.2			2.7
9	3.2			0.3		
10	5.7			0.2		
11	25.3			1.6		
12	15.6			3.4		
13	70.4			13.6		
14	54.9			6.3		
15	9.0			0.2		
16	56.0			2.2		
17	8.2			2.3		
18			4.7			15.7
19			3.4			17.2
20			2.3			6.1
Mean densities	21.1	6.9	3.2	2.8	4.5	10.4

The highest densities of large rockfish observed from the submersible were at trawlable sites. Densities averaged 21.1 rockfish/1000 m^2 of seafloor area at the 13 trawlable sites compared with 6.9 rockfish/1000 m^2 at the 3 marginally-trawlable sites and 3.2 rockfish/1000 m^2 at the 4 untrawlable sites (Table 3). About 90% (3565) of the large rockfish were associated with pebble substrate on flat or low-relief bottom. The remaining 455 large rockfish were among a variety of rugged habitats: 226 (6%) over cobble at trawlable sites, 138 (47%) over cobble and boulders at marginally-trawlable sites, and 91 (62%) among ledges, coral, etc., at untrawlable sites (Table 4). The preference of trawlable substrate by Pacific ocean perch is supported by two other studies: Westrheim (1970) mentions that best trawl catches of Pacific ocean perch were on "good bottom"; and Matthews et al. (1989) used sunken gill nets and caught 231 Pacific ocean perch (38% of the rockfish catch) on trawlable bottom, but only 25 (2% of the rockfish catch) on untrawlable bottom.

Only trawlable sites contained high densities of large rockfish, but densities varied considerably among trawlable sites. For example, sites 6 and 7 were 55.2 km apart and had a sixfold difference in large-rockfish densities; adjacent sites 16 and 17, only 2.8 km apart, had a sevenfold difference in large-rockfish densities (Table 3). These variations in abundance may have been related to the distribution of cobble habitat: All groups of more than 30 large rockfish were within 20 m of cobble habitat, although cobble averaged only 10% of the habitat at trawlable sites. The cobble was in patches <30 m^2 and the cobble size was <0.5 m in diameter.

Distribution of small rockfish

Of the small rockfish, 68% (781) were in groups of 2–60 individuals and 32% (360) were solitary (Table 2). Distribution by group size of 2–10, 11–50, and 51–200 rockfish was 41%, 52%, and 7%, respectively. Individuals within a group were usually separated by <1 m; small rockfish, in contrast to large, did not seem to orient with the current.

The highest densities of small rockfish were at untrawlable sites. Their densities averaged 10.4 rock-

Table 4

Percent rugged habitat, and proportions of large and small rockfish using rugged habitat at 20 submersible dive sites in the eastern Gulf of Alaska. Rugged habitat consisted of cobble at trawlable sites (T), cobble and boulders at marginally-trawlable sites (MT), and ledges, coral, etc., at untrawlable sites (U).

		Rockfish using rugged habitat/Rockfish total (*N*)					
	% rugged	Large			Small		
Site	habitat	T	MT	U	T	MT	U
1	6		5/47			18/30	
2	33		64/138			95/129	
3	31		69/110			22/30	
4	38	12/53			39/46		
5	10	33/110			4/10		
6	9	1/20			15/22		
7	3	11/187			4/4		
8	21			16/20			17/24
9	4	2/42			1/4		
10	2	2/78			3/3		
11	4	40/351			16/22		
12	6	0/189			39/41		
13	25	92/845			158/163		
14	12	13/675			77/78		
15	1	0/94			0/2		
16	18	19/829			32/32		
17	5	1/106			15/30		
18	76			26/55			153/185
19	49			36/41			193/206
20	74			13/30			64/80
Total numbers		226/3579	138/295	91/146	403/457	135/189	427/495
Percentages		6%	47%	62%	88%	71%	86%

fish/1000 m^2 of seafloor area at the four untrawlable sites, compared with 4.5 rockfish/1000 m^2 at the three marginally-trawlable sites and 2.8 rockfish/1000 m^2 at the thirteen trawlable sites (Table 3). Most small rockfish were over rugged habitat: 88% (403) over cobble at trawlable sites, 71% (135) over cobble and boulders at marginally-trawlable sites, and 86% (427) among ledges, coral, etc., at untrawlable sites (Table 4). Small-rockfish densities were minimal estimates because rugged habitat blocked some fish from the observer's view. Three other submersible studies noted use of rugged habitat by small rockfish: Carlson & Straty (1981), Straty (1987), and Pearcy et al. (1989).

Trawl catches

Seven trawlable sites and two marginally-trawlable sites were sampled with bottom trawls. Trawl speed ranged from 5.5 to 6.5 km/h, and the trawl intersected at least three of the four submersible transect paths at each of the nine sites (Fig. 3). Total number of fish captured was 11,089; 65% (7162) were rockfish (Table 5). Of the rockfish, 81% were Pacific ocean perch: 5587 adults (>25 cm) and 219 juveniles (≤25 cm). After trawl-caught rockfish were standardized to the submersible rockfish categories, large rockfish, small rockfish, and other rockfish comprised 90%, 9%, and 1% of the trawl-caught rockfish, respectively. Other commonly occurring fish in the trawl hauls were shortspine thornyhead (17%), flatfish (13%), and walleye pollock (3%) (Table 5).

The composition of fish captured in trawls and observed from the submersible were highly correlated; correlation coefficients (r) for all rockfish combined, shortspine thornyhead, flatfish, and walleye pollock were 0.93, 0.86, 0.79, and 0.72, respectively (Fig. 4). These high correlations indicate that bottom trawls sampled the same fish species observed from the submersible.

Catch efficiency on rockfish

Catch densities of large rockfish were highly correlated with observed densities from the submersible (r=0.88). Catch densities were

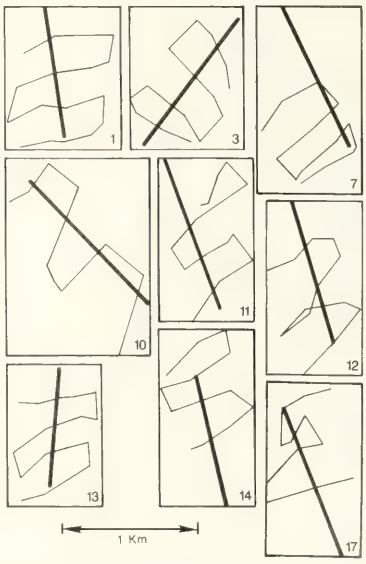

Figure 3

Submersible transect courses (—) and trawl paths (–) at nine submersible sites where rockfish counts made from a submersible were compared with CPUE of bottom-trawl hauls, August 1989. Numbers refer to sites in Figure 1.

Table 5

Numbers of rockfish and other fish captured with bottom trawls at nine submersible dive sites in the eastern Gulf of Alaska.

Site	Site type*	Area trawled ($10 m^2$)	Rockfish	Thorny-heads	Flatfish	Pollock	Other	Total
1	MT	13.7	75	32	94	4	6	211
3	MT	15.3	138	239	43	0	52	472
7	T	16.1	342	112	53	6	16	529
10	T	18.9	358	448	58	6	20	890
11	T	16.4	1148	321	139	66	15	1689
12	T	16.4	863	355	210	24	22	1474
13	T	13.0	2918	188	320	90	50	3566
14	T	14.0	893	90	183	20	20	1206
17	T	15.5	427	87	391	142	5	1052
		Totals	7162	1872	1491	358	206	11,089

*MT = marginally-trawlable site; T = trawlable site.

ments in response to trawling have been reported for other semi-demersal fish species (Wardle 1983 and 1986, Ona & Godo 1990). The low catch rates at the two marginally-trawlable sites may reflect decreased trawl efficiency in rugged habitat.

Catch densities of small rockfish were also highly correlated with observed densities from the submersible (r=0.89). Catch densities were similar to observed densities at all nine sites (Fig. 5); the ratio estimate of catch-to-observed densities was 1.3:1 (SE=0.3). Two possible reasons that ratio estimates were lower for small rockfish than for large rockfish are that (1) small rockfish escape through net meshes at a greater

higher than observed densities at the seven trawlable sites (Fig. 5) and lower at the two marginally-trawlable sites; the ratio estimate of catch to observed densities was 2.2:1 (SE=0.4). This high ratio estimate indicates that bottom trawls are very efficient for capturing large rockfish, resulting in density estimates approximately twice those observed from the submersible.

Herding of large rockfish toward the net opening may explain the high catch rates of large rockfish. Submersible counts included rockfish to 7 m off bottom, whereas the trawl sampled to only 2 m off bottom. Rockfish apparently moved downward in response to the trawl gear. Downward movements alone would have resulted in a catch-to-observed ratio of about 1:1. The ratio of 2.2:1 indicates large rockfish also moved inward toward the net opening to avoid the bridles and otter doors. The bridles and doors extend approximately 7 m on each side of the 14m horizontal net opening, increasing by twofold the seafloor area swept by the trawl gear. Downward and inward move-

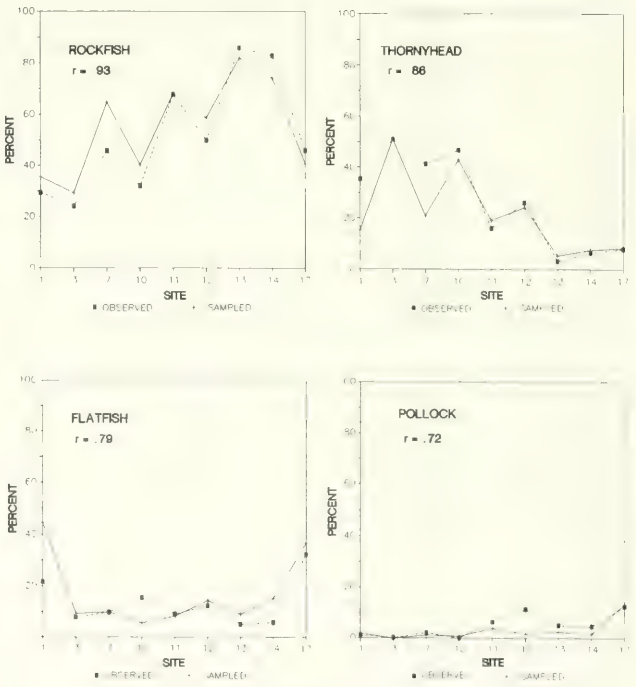

Figure 4

Percent composition of fish groups observed from a submersible and sampled with bottom trawls, and correlation coefficients (r) at nine sites in the eastern Gulf of Alaska.

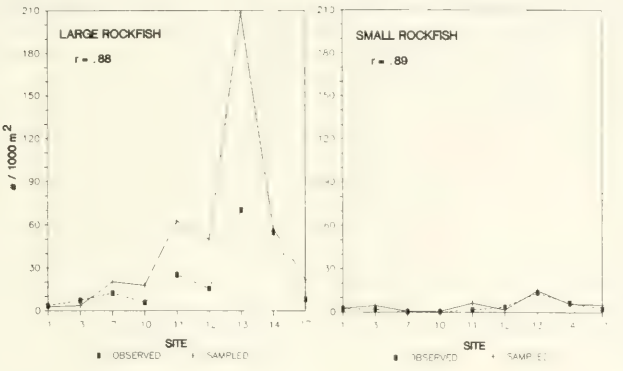

Figure 5

Densities of rockfish observed from a submersible and estimated from bottom-trawl catch rates, and correlation coefficients (r) at nine sites in the eastern Gulf of Alaska, August 1989.

rate than large rockfish, and (2) most small rockfish use rugged habitat, which bottom trawls do not sample as effectively as smooth habitat.

The 2.2:1 ratio for large rockfish and 1.3:1 for small rockfish should be considered preliminary, because these are based on only nine comparisons and the area sampled by the trawl may be underestimated. If rockfish were captured during trawl retrieval, the area sampled was underestimated and the ratios would be less. Studies are planned to determine the sampling capabilities of the trawl during retrieval, and to increase the number of trawl-to-submersible comparisons.

Reliability of fish counts

Fish densities were determined from the submersible by counting fish within an estimated distance. Estimates to within 1 m were possible because of uniform illumination and minimal change in water clarity between sites. Large rockfish were ideal for counting within the illuminated area because they were brightly colored, solitary or loosely grouped, not obstructed by rugged habitat, and usually motionless. The only movements were by individuals moving out of the direct path of the submersible, and a few larger groups moving toward the submersible. These fish swam slowly and maintained their spacing and orientation. The pilot observed similar rockfish behavior completely around the submersible. The species and size of rockfish captured in the trawls confirmed that most large rockfish observed from the submersible were adult Pacific ocean perch; 81% of the rockfish catch were Pacific ocean perch, of which 92% were >30 cm long.

Besides large rockfish, shortspine thornyhead were ideal for counting because they were motionless on the bottom and not obstructed by rugged habitat. Counts were biased for other fish species observed from the submersible. Small rockfish and "other" rockfish were underestimated because some were blocked from view by rugged habitat. Flatfish were underestimated because they blended into the bottom and were difficult to see more than about 3 m from the submersible. Walleye pollock and sablefish *Anoplopoma fimbria* reacted both positively and negatively to the submersible, and the accuracy of their counts could not be determined.

Application to bottom trawl assessments

Estimates of rockfish abundance derived from bottom trawl assessments are based on the assumptions that rockfish densities at untrawlable sites are similar to their densities at trawlable sites, and that the seafloor area sampled is determined from the horizontal opening of the net. Results from this study indicate these assumptions are incorrect for Pacific ocean perch. High densities of adult Pacific ocean perch were observed only at trawlable sites; hence, extrapolation of catch rates from trawlable substrate to untrawlable substrate would overestimate their abundance. Also, seafloor area sampled may include area swept by the bridles and otter doors, resulting in additional overestimates of abundance.

Acknowledgments

I thank the crews of the submersible *Delta* and the support vessel *Wm. A. McGaw* for completing safe and successful dives under adverse weather conditions. I thank the crew and scientists aboard the NOAA RV *Townsend Cromwell* for their detailed sampling that allowed comparisons of bottom-trawl catches to sub-

mersible observations. I also thank Victoria O'Connell of the Alaska Department of Fish and Game and John Karinen for participating in the submersible diving, and Dr. Richard Carlson and Nancy Maloney for their advice and assistance in writing this paper. The *Delta* was chartered by NOAA's National Undersea Research Program (NURP).

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Abstract.–Along the U.S. east coast, the bluefish *Pomatomus saltatrix* spawns in offshore continental shelf waters during at least two distinct periods: spring and summer. Juveniles migrate to inshore nurseries where they complete the first growing season. Previous studies have shown that diet during the oceanic larval stage consists of copepods, while older juveniles captured inshore feed largely on teleost prey. To determine timing of the ontogenetic shift in diet to piscivory, we examined the feeding habits of 189 early-juvenile bluefish (18–74 mmTL). Samples were collected from continental shelf waters of the Middle Atlantic Bight (MAB) during spring and summer of 1988 and 1989. Spring- and summer-spawned *P. saltatrix* differed in body size, prey size, and in the proportions of prey types consumed. Copepods were the most common prey type in fish <60 mm. Teleost prey appeared initially in the diet of 30 mm individuals and became the major dietary item in spring-spawned fish >40 mmTL. Gut fullness and incidence of piscivory peaked in late afternoon and were positively correlated with daylight hours. There was no evidence of an abrupt increase in mouth width associated with this ontogenetic shift in diet. Because juvenile bluefish migrate inshore soon after becoming piscivores, their impact as predators on the abundance of other young fishes is probably focused on inshore/estuarine, rather than offshore species.

Ontogenetic shift in the diet of young-of-year bluefish *Pomatomus saltatrix* during the oceanic phase of the early life history*

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The bluefish, *Pomatomus saltatrix* (Linnaeus), occurs along the Atlantic coast of North America from Florida to the Gulf of Maine. Throughout its range the species is found from shallow coastal waters to the outer, continental shelf at various times of the year (Bigelow & Schroeder 1953, Lund & Maltezos 1970, Kendall & Walford 1979, Nyman & Conover 1988). *Pomatomus saltatrix* is an important component of the recreational fishery along the east coast of North America (NMFS 1991).

Two major spawning concentrations exist in the western Atlantic. Spring spawning occurs in the South Atlantic Bight (SAB) during March–May, with a peak in April. Summer spawning occurs in the Middle Atlantic Bight (MAB) during the months of June–September, with a peak in July (Kendall & Walford 1979, Nyman & Conover 1988, McBride & Conover 1991).

The spring-spawned larvae move northeastward in waters associated with the Gulf Stream. Juveniles cross shelf waters at an age of 40–70 d, and enter bays and estuaries of the mid-Atlantic coast in late spring (Kendall & Walford 1979, Nyman & Conover 1988). Summer-spawned larvae may either spend most of the summer at sea or inhabit the inshore nursery areas of the MAB for a brief period before the onset of autumn, when both cohorts move southward to wintering grounds in the SAB (Kendall & Walford 1979, Nyman & Conover 1988).

Once inshore, *P. saltatrix* feed almost exclusively on piscine prey (Lassiter 1962, Richards 1976, Naughton & Saloman 1978, McDermott 1983, Smale & Kok 1983, Smale 1984, Olla et al. 1985, Friedland et al. 1988). Very little is known, however, about the diet of young *P. saltatrix* at sea. In the only published account, the diet of newly-hatched *P. saltatrix* was found to consist mainly of copepods (Kendall & Nalpin 1981). Hence, at some point during ontogeny there must be a shift in diet from zooplankton to fish. If the diet shift occurs early in development, then juvenile *P. saltatrix* may be important predators of larval fishes on the shelf. On the other hand, the shift from a zooplankton to a fish-dominated diet may occur coincidentally with the habitat shift to estuarine waters.

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*Contribution 866 of the Marine Sciences Research Center, State University of New York at Stony Brook.

In this paper we examine the feeding ecology of young juvenile *P. saltatrix* prior to their arrival in the nursery areas of the MAB. We document the predator size at which teleost prey initially appear in the diet and whether or not this shift to piscivory occurs coincidentally with the habitat shift inshore. Since fish are considered gape-limited predators (Hartman 1958, Ross 1978, Hunter 1980, Roberts et al. 1981), we examine mouth width for abrupt changes that may accompany an ontogenetic shift in diet.

Methods

Field collections

Spring- and summer-spawned juvenile *P. saltatrix* were sampled from transects across the MAB in 1988 and 1989. The area sampled extended along the eastern U.S. coast from Cape May, New Jersey northeast to Montauk, New York and to 125 miles offshore. Cruises were conducted during two time-periods: 4 April 1988–8 August 1988, and 4 April 1989–8 August 1989. A total of 275 stations were sampled during 16 cruises. Juvenile *P. saltatrix* were collected at 46 of these stations (Figs. 1,2). Offshore stations were located 10 nmi (18.52 km) apart, and several coastal stations were located within 1 mi (1.85 km) of the shoreline (for comprehensive cruise track maps, see Hare & Cowen 1991, Marks 1991). Cruise duration was 3–7 d with tows conducted at regular intervals, 24 h/d. Tows consisted of a 10 min net deployment filtering approximately 3500 m^3 of seawater, at a ship speed of 3–4 kn.

Samples were collected using a modified Methot Frame Trawl (Methot 1986). The opening of the trawl was 5 m^2 and the mesh was 2 mm. Total net length was 13 m. Because juvenile *P. saltatrix* are often found near the surface (Kendall & Nalpin 1981, Collins & Stender 1987), trawls were conducted with the top 30 cm of the net above the water surface. All specimens were preserved in 70% ethanol.

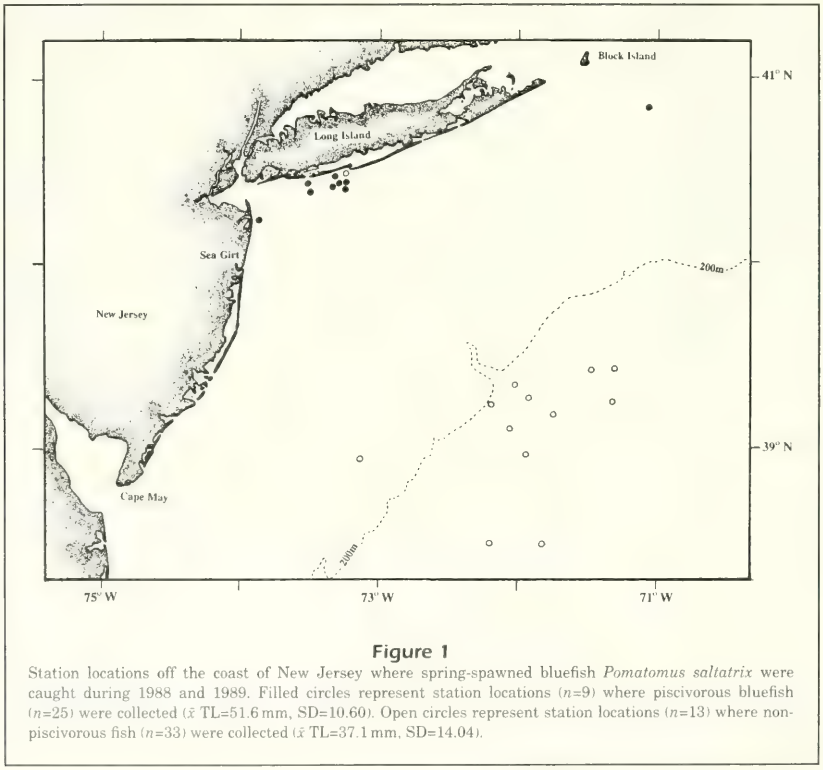

Figure 1

Station locations off the coast of New Jersey where spring-spawned bluefish *Pomatomus saltatrix* were caught during 1988 and 1989. Filled circles represent station locations (n=9) where piscivorous bluefish (n=25) were collected ($\bar{x}$ TL=51.6 mm, SD=10.60). Open circles represent station locations (n=13) where non-piscivorous fish (n=33) were collected ($\bar{x}$ TL=37.1 mm, SD=14.04).

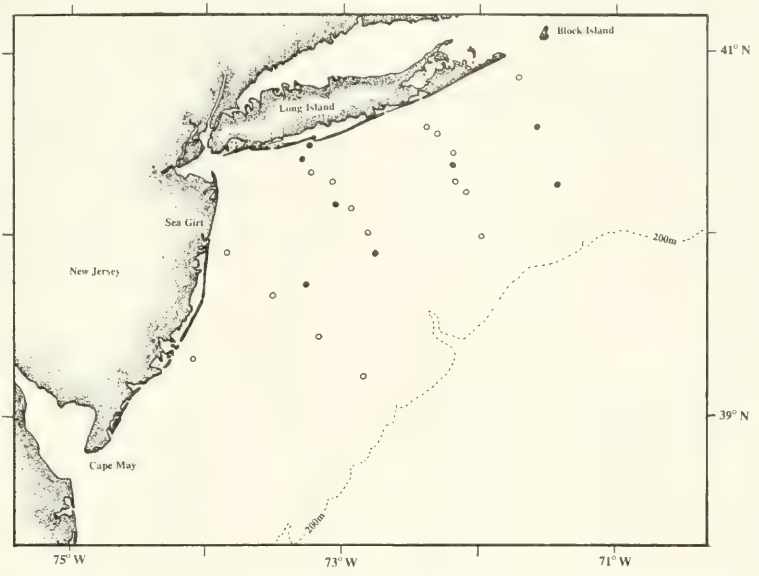

Figure 2

Station locations where summer-spawned bluefish *Pomatomus saltatrix* were caught during 1988 and 1989. Filled circles represent station locations (n=9) where piscivorous bluefish (n=18) were collected ($\bar{x}$ TL=41.0 mm, SD=7.71). Open circles represent station locations (n=16) where non-piscivorous fish (n=80) were collected ($\bar{x}$ TL=33.7 mm, SD=7.42).

Laboratory analysis

Preserved *P. saltatrix* were wet weighed (±0.001 g) and measured (total length, TL, to ±0.1 mm). Fish in the 18–74 mm size-range were examined for diet comparisons. The minimum size represents the stage at which metamorphosis into the juvenile phase is completed (Norcross 1974). The maximum fish size represents the largest specimen collected.

Stomachs were removed from the pharynx and anterior to the intestine, cut longitudinally, and the contents transferred to a petri dish. The gut cavity was then washed to remove any adhering particles. Prey items were identified to species or lowest taxon possible, enumerated, and measured for total length using a dissecting scope equipped with an ocular micrometer.

Weighted mean prey length was calculated for each stomach to provide an accurate representation of prey length consumed. Individual bluefish often consumed several small prey (e.g., copepod) and one large prey (e.g., teleost). Computation of the weighted mean is equivalent to adding up all the original measurements and dividing the sum by the total number of measurements. Hence, the most common prey type will influence the weighted mean length in proportion to its numerical occurrence (see Sokal & Rohlf 1981).

Protocol for determining various prey length was defined as follows: (1) largest diameter for hydrated oocytes, (2) metasome + cephalosome for copepods, (3) anterior edge of head to anterior edge of caudal rami for fish lice (*Caligus* spp.), (4) anterior edge of eye to anterior edge of uropod for amphipods, (5) base of rostrum to anterior edge of telson for other crustacea, and (6) total length for polychaetes, ostracods, pteropods, squid (*Loligo* spp.), and teleost prey.

Fish scales were present in <5% of the guts and were not regarded as a prey type, but were used to indicate the occurrence of piscine prey. The presence of any teleost part (e.g., otolith, spine, fin ray) was recorded as piscine prey.

Prey dry weights were obtained either from the literature or measured directly after oven-drying for 24 h at 60°C. Where individual prey weights were very low or existed as exoskeleton material, dry weights were obtained by drying a known number of fresh prey items to obtain an average weight per prey item (see Grossman 1980, Ryer & Orth 1987).

Dry weights of 49 bluefish (17–74 mm) with empty guts were determined by oven-drying at 60°C until recording constant weight. The time required for a constant measure was 24–48 h, depending on individual fish size. The regression equation (Log Y=3.128 × Log X–6.059) was used to predict the dry weights of all bluefish in this study (Marks 1991). Gut fullness was measured using a ratio of prey dry weight to individual *P. saltatrix* dry weight.

Mouth width measurements were taken to detect morphological changes during ontogeny. Mouth width was measured as the width at the posterior tip of the maxillaries using digital calipers (±0.01 mm) (see Hartman 1958, Ross 1978, Hunter 1980, Hunter & Kimbrell 1980). Additionally, body depth of prey fish was measured at the widest location.

Diet analysis

Diet was analyzed using the methods outlined by Hyslop (1980) (see also Lassiter 1962, Naughton & Saloman 1978, Friedland et al. 1988): Total number of stomachs in which a food item occurred divided by the total number of stomachs (%F); total number of individuals of a taxon divided by the total number of food items (%N); and total dry weight of a taxon divided by the total dry weight of all food items (%W).

Bluefish were grouped by spring- and summer-spawned cohorts based on size and date of capture (Kendall & Walford 1979, Nyman & Conover 1988, McBride & Conover 1991). Trophic ontogeny was examined by arbitrarily splitting bluefish into size groupings and using percent dry weight of prey categories to assess dietary importance.

Results

General diet description

A total of 189 *P. saltatrix* were examined for gut content (Table 1). Approximately 84% had food present in the stomachs. Spring-spawned bluefish consumed an average of 31 prey items per individual compared with 85 prey items for summer-spawned fish.

Spring-spawned fish were found to be significantly larger (Table 1; *t*-test for means with unequal variances, t_s=5.24, df=156, $P \leq 0.001$,) and had a greater mouth width ($0.01 < P < 0.05$, t_s=2.39) than did summer-spawned fish.

Overall, copepods were the dominant prey, accounting for 50% and 94% of the diet by weight (Table 2) of

Table 1

Comparison of sample characteristics from the spring- and summer-spawned cohorts of *Pomatomus saltatrix*. (*$0.01 < P < 0.05$, ***$P < 0.001$; numbers in parentheses are ±1SD.)

Sample characteristics	Spring-spawned	Summer-spawned
Sample size	63	126
Percentage with prey	92	79
Mean mm TL (±1SD)	42.9 (14.57)	34.7 (7.84)***
Size range (mm)	19.0–74.0	18.0–64.0
Mean mouth width (mm)	2.38 (1.040)	2.05 (0.499)*
Mouth width range (mm)	0.85–5.18	0.99–3.93
Mean prey length (mm)	2.67 (2.548)	1.12 (0.565)***
Prey length range (mm)	0.27–36.0	0.29–12.62

Table 2

Stomach contents of spring- and summer-spawned juvenile bluefish *Pomatomus saltatrix* collected in the Middle Atlantic Bight. (%F=percent frequency of occurrence; %N=percent numerical abundance; %W=percent dry weight).

	Spring-spawned			Summer-spawned		
Prey taxa	%F	%N	%W	%F	%N	%W
Polychaeta						
Unidentified Maldanidae	1.7	0.0	0.0	0.0	0.0	0.0
Crustacea						
Calanoid copepods	89.7	88.6	50.0	99.0	97.6	93.9
Cyclopoid copepods	1.7	0.0	0.0	0.0	0.0	0.0
Fish lice (*Caligus* spp.)	1.7	0.0	0.0	0.0	0.0	0.0
Ostracods	8.6	2.0	1.1	4.0	0.1	0.2
Gammarid amphipods	5.2	0.2	0.7	1.0	0.0	0.1
Hyperiid amphipods	1.7	0.0	0.1	5.0	0.1	0.8
Mysid shrimp	3.4	0.1	0.1	1.0	0.0	0.0
Lucifer shrimp (*Lucifer* spp.)	1.7	0.0	0.1	4.0	0.0	0.1
Euphausids	3.4	0.1	0.1	7.0	0.1	0.2
Zoea	34.5	4.4	5.3	4.0	0.1	0.2
Megalopae	19.0	1.4	3.7	1.0	0.0	0.0
Unidentified crustacea	1.7	0.1	0.1	5.0	0.0	0.1
Gastropoda						
Unidentified pteropod	0.0	0.0	0.0	1.0	0.0	0.0
Cephalopoda						
Squid (*Loligo* spp.)	0.0	0.0	0.0	1.0	0.0	0.1
Teleostei						
Fish larvae and juveniles	39.7	1.9	37.5	17.0	0.2	1.8
Fish eggs (Unidentified)	17.2	0.9	0.8	37.0	1.6	2.4

spring- and summer-spawned fish, respectively. Teleosts were the next most-abundant prey type. Fish prey constituted 37% by weight of the diet of spring-spawned bluefish. Summer-spawned bluefish, by comparison, consumed a much smaller amount (1.8%). The majority of teleosts consumed were hakes (*Urophycis* spp.) or other unidentifiable gadids. There were also limited occurrences of engraulids and triglids (*Prionotus* spp.). Based on number and weight, all other prey types were relatively unimportant except crab larvae (zoea and megalopae). A low proportion by weight was comprised of hydrated oocytes which were frequently present in stomachs. Rare prey included *Caligus* spp., *Loligo* spp., a maldanid polychaete and a pteropod.

Onset of piscivory

We pooled data by size-class within cohorts to provide an overall view of diet changes with body size. The smallest size-class of summer-spawned *P. saltatrix* (17–29.9 mm) fed exclusively on copepods and fish eggs (Fig. 3). The 30.0–39.9 mm size-class expanded their diet to include teleosts, amphipods, and miscellaneous crustaceans. Bluefish in the 40.0–49.9 mm class also

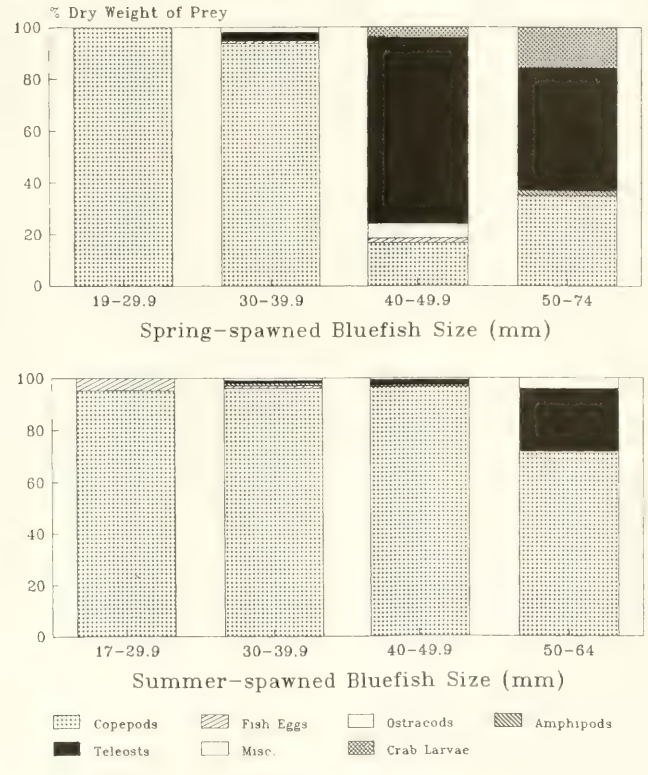

Figure 3

Trophic ontogeny of four bluefish *Pomatomus saltatrix* size-classes for spring- and summer-spawned cohorts expressed as the % dry weight of prey. (Misc. category includes ostracods, fish eggs, misc. crustaceans, and amphipods). Sample sizes for each size-class (smallest to largest) were: summer-spawned fish, n = 25, 47, 25, 3; spring-spawned fish, n = 10, 19, 12, 18.

continued to feed mostly on copepods. The largest size-class of summer-spawned bluefish increased their consumption of fish prey and continued to take copepods and miscellaneous crustaceans.

The diet of spring-spawned bluefish (19.0–39.9 mm) was similar to the diet of same-sized fish from the summer-spawned cohort. There was a marked difference, however, in the amount of fish prey consumed by the 40.0–49.9 mm size-class. This difference was also evident in the largest size-class, despite small sample sizes in both cohorts. The diet of the two largest size-classes of spring-spawned bluefish also contained a relatively high percentage of crab larvae.

Mean prey length increased significantly with predator size in both spring- and summer-spawned bluefish (Fig. 4). Variance about the regression, however, was much greater for spring-spawned fish. Since transformation did not correct for inequality in the variances, we did not attempt further statistical analyses of these data.

Bluefish belonging to the spring-spawned cohort were caught either close to shore (<8 km) or at distances >100 km from shore (Fig. 1). Piscivorous individuals from this cohort were larger in size ($\bar{x}$ TL=51.6 mm) and generally captured closer to shore than non-piscivorous individuals ($\bar{x}$ TL=37.1 mm). The difference between the mean TL for piscivorous fish versus non-piscivorous fish was significant ($P<0.001$, df=50, $t_s=6.22$).

In comparison, piscivorous bluefish from the summer-spawned cohort were more evenly dispersed across the shelf (Fig. 2). Mean TL of piscivorous individuals (41.0 mm) was significantly greater than that of non-piscivorous fish ($\bar{x}$ TL=33.7, $P<0.001$, df=92, $t_s=5.04$).

Pomatomus saltatrix tended to feed on larger teleost prey with increasing size. A linear regression of prey fish length on predator length was highly significant ($r^2=0.46$, $n=25$, $P\leq0.001$; Fig. 5). With increasing body size, *P. saltatrix* also tended to feed on multiple teleost prey. More than one fish prey was found only in *P. saltatrix* >49 mm. The maximum number of intact teleost prey found in an individual predator (49 mm) was three. A *t*-test for the difference in means between the size of fish that consumed multiple fish prey (57.1 mm) and the size of those that fed on single prey (44.8 mm) was significant ($P<0.05$, df=30, $t_s=3.265$).

Diel cycle

Gut fullness pooled across all fish examined in the study versus time of day is depicted in Fig. 6. Gut fullness was evaluated as the ratio of total prey dry weight to individual *P. saltatrix* dry weight (×100). Feeding peaked during 1600–2000 h (the time of sunset during the study period ranged from 1945 to 2020 h). A nonparametric Spearman Rank Correlation test (Sokal & Rohlf 1981) resulted in a significant, positive relationship ($r_s=0.5818$, $P\leq0.001$, $n=189$) between time of day and gut fullness. The high proportion of food in the gut at approximately 2400 h may be attributed to food that was consumed during the evening crepuscular period, since prey from this time-period were generally in an advanced stage of digestion. Experimental laboratory data

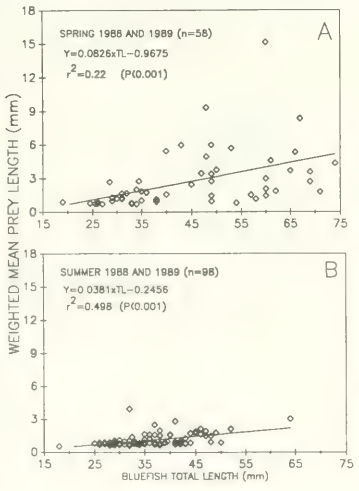

Figure 4
Regressions of weighted mean prey total length (mm) on bluefish *Pomatomus saltatrix* total length (mm) for spring-spawned **(A)** and summer-spawned **(B)** bluefish.

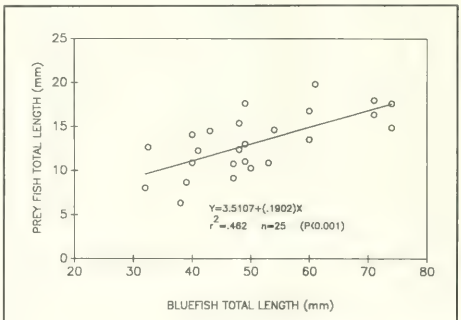

Figure 5
Regression of prey fish total length (mm) on bluefish *Pomatomus saltatrix* total length (mm).

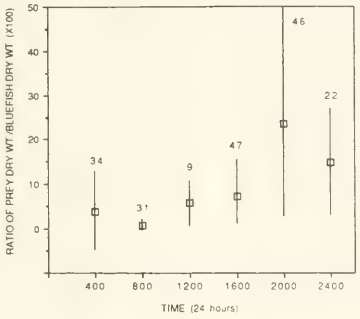

Figure 6

Gut fullness expressed as a ratio of total prey dry weight (g) divided by individual dry weight (g) (×100) for bluefish *Pomatomus saltatrix*, as a function of time of day. Squares represent the mean; vertical lines represent ±1SE. Sample sizes are provided above each vertical line.

showed that time to 90% digestion at 21°C is 5–7 h post-feeding in 57–199 mm bluefish (Marks 1991).

A two-way test for independence (adjusted G-statistic, G_{adj}=5.98, P<0.05; Sokal & Rohlf 1981) showed that the occurrence of fish in the stomachs depended on time of day. Piscivory was restricted to daylight hours, with some incidence recorded prior to 2400 h but none during 2400–0400 h. A slight increase (12%) was observed at 0800 h; the maximum evidence of piscivory (42%) occurred at 1600 h.

Mouth morphology

Teleost prey had the greatest maximum thickness of all prey types. The relationship between thickness of fish prey at the widest point and *P. saltatrix* mouth width was positive, but the regression was marginally non-significant (P=3.91, n=23, 0.05<P<0.1).

The log-log regression of mouth width on total body length was highly significant (r^2=.857, n=203, P<0.001) and showed no evidence of an abrupt change in mouth width coincident with the onset of piscivory (Fig. 7). The regression slope (1.06) suggests isometric growth of mouth width in relation to body size. A SYSTAT piecewise linear-regression procedure (Wilkinson 1987) was employed to test

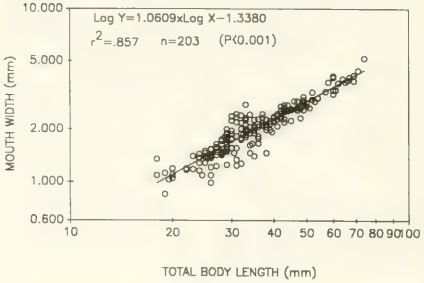

Figure 7

Regression of mouth width (mm) on total length (mm) for bluefish *Pomatomus saltatrix*.

for the existence of more than one slope in the line. The test was run with an undetermined intersection as well as with an *a priori* intersection at 30 mm (the size of initiation of piscivory). No significant differences in slope were observed, and the conclusion was that a single regression line adequately described the relationship between mouth width and total body length.

Discussion

Our results indicate that during the oceanic phase of the early life history, *P. saltatrix* gradually shifted its diet from small prey (crustaceans, mainly copepods) to fish and crab larvae. The diet appeared to shift over a size range that corresponds to the period of inshore migration.

The smallest juvenile *P. saltatrix* foraged predominately on copepods. A diet high in crustacean prey is characteristic of the larval and juvenile phases of many piscivorous fishes, including the Atlantic cod *Gadus morhua* (Last 1980) and the largemouth bass *Micropterus salmoides* (Keast 1985).

Overall, fish prey became a substantial component of the diet at about 40–60 mm. The majority of teleosts consumed were hakes (*Urophycis* spp.) or other unidentified gadids. Gadids are among the most-abundant icthyoplankton group found in the MAB during the spring (Kendall & Nalpin 1981, Morse 1989, Cowen et al. In press).

Crab larvae initially appeared in the diet of bluefish <40 mm and accounted for 9% of the diet by weight in bluefish >60 mm (Fig. 4). The appearance of crab larvae as the third most-abundant prey item is not surprising. The majority of crab larvae were found in spring-spawned bluefish captured close to shore. This may be a result of higher concentrations of crab larvae at frontal zones in the nearshore environment. Friedland et al. (1988) reported a high abundance of crustaceans in the diet of inshore juveniles.

There was a marked increase in the maximum size of prey consumed as spring-spawned bluefish size increased beyond 30 mm (Fig. 3). This is in agreement with the generalization that prey size increases with increasing predator size in fishes (Brooks & Dodson 1965, Tyler 1972, Ross 1977 and 1978, Hunter & Kimbrell 1980, Roberts et al. 1981, Smale 1984, Ryer & Orth 1987, Wetterer 1989, Persson 1990). There was, however, only a moderate increase in the maximum prey sizes consumed by summer-spawned bluefish. The reasons for this discrepancy are not clear, but may be a function of prey availability and differences in size at inshore migration. Summer-spawned bluefish appear inshore at smaller sizes than do spring-spawned bluefish (McBride & Conover 1991). The shift to larger prey items in summer-spawned fish may occur after inshore migration.

The onset of piscivory in the 30–70 mm size-range is similar to that reported for other teleosts: 40–60 mm for characids and 60–80 mm for pimelodids (Winemiller 1989), 23 mm for *Micropterus salmoides* (Keast 1985), and 60–100 mm for *Gadus morhua* (Bowman & Michaels 1984).

Piscivory in larval stages has been reported in some fishes, but apparently does not occur in bluefish. Hunter & Kimbrell (1980) found *Scomber japonicus* to be piscivorous at 8 mmSL. This could perhaps be attributed to the large mouth and strong, well-developed jaws that are characteristic of larval scombrids (Fahay 1983). Hunter (1980) also reported *Sphyraena argentea* to be piscivorous at 4.4 mm. Houde (1972) found evidence for piscivory in *S. borealis* at 9 mm. Despite having well-developed dentition at 4.3 mm (Fahay 1983), larval and postlarval *P. saltatrix* may lack either the jaw structure, visual acuity, or swimming speed necessary to feed on other fishes.

Pomatomus saltatrix are known to be visual predators (Olla & Marchioni 1968, Olla et al. 1970, Van der Elst 1976). It follows that reduced light levels after the evening crepuscular period should reduce feeding efficiency. Olla & Marchioni (1968) documented that *P. saltatrix* detect and attack prey visually, so it is not surprising that feeding appears to be correlated with daylight periods. Kjelson et al. (1975) also reported finding the lowest proportion of food in the gut of postlarval fishes during the evening hours.

Fish are considered "gape-limited" predators and are ultimately restricted by mouth size (Hartman 1958, Ross 1978, Hunter 1980, Roberts et al. 1981). Ontogenetic shifts in diet may be related to morphological changes in mouth size during development that allow for consumption of larger prey (Ross 1978, Grossman 1980, Roberts et al. 1981). Mouth width in *P. saltatrix*, however, appears to increase isometrically with body size. The inclusion of fish in the diet at a size of 30 mm may be attributed to changes in feeding behavior with growth, or simply a result of the mouth reaching a size that permits fish ingestion.

The size at which teleost prey constitute a substantial portion of the diet is about 40–70 mm. This is also the size-range in which *P. saltatrix* juveniles recruit to the inshore waters of the MAB (Nyman & Conover 1988, McBride & Conover 1991). Hence, the dietary shift is largely coincident with a habitat shift. This is further supported by the observation that virtually all piscivorous spring-spawned *P. saltatrix* were captured close to shore. The limited occurrences of piscivory in the summer-spawned cohort were more evenly dispersed across the shelf. However, summer-spawned bluefish migrate inshore at a smaller size than do spring-spawned fish (McBride & Conover 1991) and may do so largely before the onset of piscivory. Our results suggest that the overall impact of predation by young bluefish on the abundance of other fishes is probably focused more on inshore rather than offshore species.

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Trawl survey estimation using a comparative approach based on lognormal theory*

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Abstract.–The spatial distributions of marine biota are frequently patchy. Samples taken from these populations are characterized by values which are mostly small, relative to the population mean, and a few that are very large. It is therefore difficult to estimate stock size using conventional methods. We performed Monte Carlo simulations based on trawl data for Dungeness crab *Cancer magister* and compared the behavior of three estimators of central tendency: sample mean, geometric mean, and a lognormal estimate. Although the sample mean is unbiased, results indicate that single estimates of the population mean (and thus population estimates obtained using area-swept) may be overly sensitive to extreme values; confidence intervals are large and capture the true value at a level well below that prescribed. Estimates of the geometric mean exhibit more stable behavior about its parameter, with mixed results for the lognormal estimate. We propose a conservative approach based on comparison of trends found in each of the three estimators. Moreover, we suggest that abundance of aggregated stocks should be indexed with an estimator that has more desirable statistical properties, such as the geometric mean. This may reduce error associated with conventional fisheries stock-assessment practices and thus provide for more effective management of overdispersed stocks.

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Effective scientific management of fishery resources is dependent upon reliable measures of stock abundance. To this end, research trawl surveys are routinely used in concert with fishery catch statistics to provide estimates of population parameters. The analytical procedures used often rely on the assumption that statistical methods based on normal probability theory are appropriate and, as such, that the individuals comprising the population are not aggregated in space (Elliott 1977). However, marine biota are commonly overdispersed, and frequently it is the *logarithms* of abundance (or biomass) which conform to the normal or Gaussian distribution (reviewed by McConnaughey 1991). Rather than an artifact of sampling, in many cases this spatial attribute is the product of behavioral responses and/or physical processes affecting dispersal (e.g., Epifanio 1987, Dew 1990). Samples taken from these populations are characterized by mostly small values relative to the population mean, and a few very large ones. Under these circumstances, single estimates of the population mean from the arithmetic mean (sample average) may be too low because very large values are often underrepresented at the levels of sampling effort common to research trawl surveys. When large catches are present in a sample, variance estimates may become excessively high (e.g., Otto 1986). This may introduce a high degree of uncertainty into the resource management process which, if ignored, can have potentially serious repercussions (Ludwig & Walters 1981).

We investigated two alternative measures of central tendency and compared their statistical behavior with that of the arithmetic mean. These alternatives are the geometric mean and a model-based estimate of the arithmetic mean based on lognormal theory. An evaluation of trends based on a comparison of the three estimators is proposed. This approach may identify error associated with the conventional index of abundance, thereby reducing the likelihood of false conclusions concerning trends in stock abundance.

Data and methods

Monthly trawl surveys of Dungeness crab *Cancer magister* abundance along the southern Washington coast provided representative values of density (n/ha) for analysis with Monte Carlo techniques. Density data

*Contribution 853 of the School of Fisheries, University of Washington.

such as these are commonly expanded according to area-swept procedures to produce estimates of population size. Both nearshore and estuarine populations were sampled, and we examined data collected during four consecutive years. Survey design and methodology are discussed in Armstrong & Gunderson (1985) and Gunderson et al. (1990).

The spatial dispersion of a population determines the relationship between its mean abundance and variance, and this information may be used to select an advantageous data transformation (Elliott 1977). Strong linear relationships between the means and standard deviations of our density data (r^2=0.98 and 0.70, with $P \ll 0.001$ and $P \ll 0.001$ for the coastal and estuarine areas, respectively) and graphical analysis of log-transformed data suggested a logarithmic transformation would be appropriate. In order to test this assumption, the Kolmogorov test for normality was applied to the density data for each cruise, both before and after transformation (Table 1). These preliminary analyses suggested that the density data were lognormally distributed and, as such, that individuals in the crab population were aggregated in space. However, lognormal theory cannot be applied directly to any sample that contains a zero value, since the logarithm of zero is undefined. Since our data exhibit only the occasional zero catch, we used the common ln (X+1) transformation to normalize the data. An alternative approach, when a significant fraction of the data consists of zero catches, would be to use the Δ-distribution (Pennington 1983 and 1986, Smith 1988), which is essentially a lognormal distribution with a proportion (Δ) of zeros.

The lognormal distribution and parameter estimation

The lognormal distribution may be represented as a Gaussian distribution of logarithmic data or, equivalently, as a right-skewed distribution of untransformed data (Aitchison & Brown 1969). A brief review of the density function and relevant parameters for the lognormal distribution appear in the Appendix. There, and throughout the text, we use the following notation to distinguish between untransformed and transformed scales and between population parameters and their estimates: X represents untransformed density values, while $\bar{X}$ (the ordinary sample mean) and s^2_X (the

Table 1

Goodness-of-fit probabilities from Kolmogorov tests for normality with means ($\bar{Y}$) and standard deviations (s_Y) for log-transformed *Cancer magister* abundance data. Cruise refers to sequential trawl surveys (n=number of samples) in coastal and estuarine areas along the southern Washington coast over a consecutive 4-year period.

	Coast					Estuary				
Cruise	n	Raw[1]	Log[2]	$\bar{Y}$	s_Y	n	Raw	Log	$\bar{Y}$	s_Y
1	35	.006	.964	4.20	2.35	20	.211	.890	6.96	1.19
2	41	.000	.740	4.64	2.50	20	.129	.816	6.82	1.10
3	42	.000	.687	4.95	2.86	20	.909	.651	6.88	.66
4	38	.000	.738	6.65	2.13	20	.133	.207	6.59	.79
5	42	.000	.932	5.30	2.26	20	.167	.434	6.34	.56
6	44	.014	.287	3.34	1.97	16	.373	.411	4.90	1.72
7	40	.109	.230	3.08	1.72	20	.004	.418	6.04	1.21
8	41	.000	.800	3.59	1.60	20	.088	1.000	5.65	1.21
9	44	.000	.164	2.91	2.08	20	.013	.573	5.68	1.36
10	43	.016	.528	3.90	1.78	20	.140	.878	5.45	.96
11	44	.007	.102	3.16	2.10	20	.172	1.000	4.64	1.16
12	44	.002	.829	3.62	1.93	20	.129	.705	5.81	1.01
13	44	.000	.759	4.55	2.15	20	.435	.979	6.61	1.04
14	44	.000	.507	3.90	2.49	20	.311	.960	5.93	1.06
15	44	.000	.306	5.05	2.20	20	.336	.981	6.42	1.10
16	44	.000	.484	3.62	3.84	20	.027	.931	6.43	1.91
17	44	.000	.471	3.44	4.94	20	.434	.922	6.93	.82
18	44	.000	.370	3.69	4.73	19	.336	.868	6.82	1.18
19	44	.000	.949	4.75	6.89	20	.388	.980	6.43	.92
20	43	.000	.528	3.90	6.48	20	.010	.964	6.23	1.29

[1]P-value for untransformed data.
[2]P-value for log-transformed data.

sample variance) are estimators of μ and σ^2, the population mean and variance of the untransformed data. Letting $Y = \ln(X)$, $\bar{Y}$ and s^2_Y are estimators of μ_{LN} and σ^2_{LN} the population mean and variance of the log-transformed data. Note that in Eq. (A3) and (A4) both μ and σ^2 for the lognormal distribution are functions of two parameters, μ_{LN} and σ^2_{LN}, making the former parameters difficult to estimate. In particular, any estimate of μ involves both location and dispersion parameters. Therefore, variation in estimating μ will come from two sources: variation in estimating μ_{LN} and variation in estimating σ^2_{LN}.

The arithmetic mean (AM) The ordinary sample mean is an unbiased estimator of μ regardless of the underlying frequency distribution. When the underlying distribution is normal, the sample mean is also the minimum variance unbiased estimator (MVU, the one with the smallest variance of all unbiased estimators) of μ. However, the sample mean does not have this MVU property when the underlying distribution is lognormal (Gilbert 1987). Moreover, the AM is sensitive to the presence of one or more large data values, particularly for small sample sizes. For lognormal data, these extreme values are not outliers; they simply reflect the right-skewed nature of the distribution. Finney (1941) demonstrated the inefficiency of the sample mean when the variance of the natural logarithms is greater than 0.69, and Koch & Link (1970) suggested using the sample mean only when the coefficient of variation is believed to be less than 120%. For highly-skewed distributions such as the lognormal, sample sizes in excess of 200 may be necessary to invoke the Central Limit Theorem, which justifies use of the sample mean for inferences about means of populations that are not normally distributed (Sissenwine 1978, Jahn 1987).

The Finney-Sichel estimator (FM) Among alternative estimators that have been investigated is an MVU estimator of μ (Finney 1941, Sichel 1952), which also has been described as equivalent to a maximum-likelihood estimator for lognormal data (Aitchison & Brown 1969). The Finney-Sichel method adjusts the geometric mean upwards and is commonly used in gold and trace-mineral assay work, where ore concentrations are typically lognormally distributed (Sichel 1952). If $\bar{Y}$ and s^2_Y represent the ordinary sample mean and variance of the log-transformed values, the Finney-Sichel estimate for μ is

$$FM = \exp(\bar{Y})\,\psi_n(t) \qquad (1)$$

where n is the sample size and $\psi_n(t)$ is the infinite series

$$1 + \frac{(n-1)t}{n} + \frac{(n-1)^2t^2}{2!n^2(n+1)} + \frac{(n-1)^3t^3}{3!n^3(n+1)(n+3)} + \frac{(n-1)^4t^4}{4!n^4(n+1)(n+3)(n+5)} + \ldots, \qquad (2)$$

with $t = \frac{s^2_Y}{2}$. The function $\psi_n(t)$ is defined such that $E[\psi_n(s^2)] = \exp\left(\frac{n-1}{n}\sigma^2\right)$ and $\lim_{n\to\infty}[\psi_n(s^2)] = \exp(\sigma^2)$; it is used extensively with the lognormal distribution (Smith 1988). In their book, Aitchison & Brown (1969) included tables of ψ_n for computing the Finney-Sichel estimate. More extensive tables are provided in Link et al. (1971), who claim that linear interpolation between tabled values gives close approximation for estimates of μ. They also include a FORTRAN program for calculating the ψ_n function, which we used in computing FM, the Finney-Sichel estimate of the population mean. (A version of this program may be obtained from the authors.)

Confidence limits for the lognormal mean are not symmetric because of the skewed nature of the underlying distribution. Hence, it becomes necessary to compute separate upper and lower confidence limits. Land (1971, 1975) obtained upper one-sided $100(1-\alpha)\%$ and lower one-sided $100\alpha\%$ confidence limits for the lognormal mean, where α is the frequency of type I error:

$$UL_{1-\alpha} = \exp\left(\bar{Y} + \frac{s^2_Y}{2} + \frac{s_Y H_{1-\alpha}}{\sqrt{n-1}}\right) \qquad (3)$$

$$LL_{\alpha} = \exp\left(\bar{Y} + \frac{s^2_Y}{2} + S_y \frac{H_{\alpha}}{\sqrt{n-1}}\right). \qquad (4)$$

The quantities $H_{1-\alpha}$ and H_{α} [functions of α, (n–1) and s_Y] are obtained from tables in Land (1975) for sample sizes of $n \geq 3$.

The geometric mean (GM) The geometric mean, $e^{\bar{Y}}$, will be a biased estimate of μ (Appendix) but may be more precise with respect to its population parameter than will be the case for estimators of the population mean. (Actually, $E(e^{\bar{Y}}) = \exp(\mu_{LN} + \frac{1}{2n\sigma^2_{LN}}$ so the GM is biased even for $e^{\mu_{LN}}$, but this bias decreases rapidly as n increases.) When exponentiated, the population mean of the transformed data, μ_{LN}, is the geometric mean catch and, equivalently, the median catch for lognormal data. It remains unaffected by skewness, a function of $[\exp(\sigma^2_{LN}-1)]$. It is less affected by large values of X, owing to the nature of a logarithmic transformation; hence, its sampling distribution is less skewed

than that for the AM. Aitchison & Brown (1969) note that "since the arithmetic mean involves both the location and dispersion parameters, it is not a pure measure of the [response variable] under the lognormal hypothesis: for this the geometric mean or median is to be preferred."

Monte Carlo simulations based on crab trawl data

Monte Carlo simulations consist of calculations made on data sets whose elements are randomly selected from specified probability distributions. This approach permits an evaluation of various point-estimation procedures on the basis of expected outcomes. It also allows a closer examination of individual cases than is possible with a purely analytical approach and permits an evaluation of the effects of sample size. For this investigation, single values of mean density and standard deviation were calculated for each cruise in the two trawl locations along the Washington coast. The means of these statistics were used to define two representative lognormal distributions, which are identified as lognormal (4,2) for the coastal area and lognormal (6,1) for the estuarine area. These distributions have means of 4.0 and 6.0, and standard deviations of 2.0 and 1.0, respectively, for the log-transformed variable; they will be referred to as LOGN (4,2) and LOGN (6,1) (Fig. 1). From these two probability distributions, we created 1000 sets of simulated density data for each of 13 sample sizes (2,4,6,8,10,15,20,25,30,35,40,45,50) using a pseudorandom number generator (Minitab, Inc., University Park PA). Sample sizes were selected to encompass the range of values associated with ongoing trawl surveys. Table 2 presents descriptive statistics for each of these data sets. (These data sets are archived on magnetic tape, and access can be arranged through the authors.)

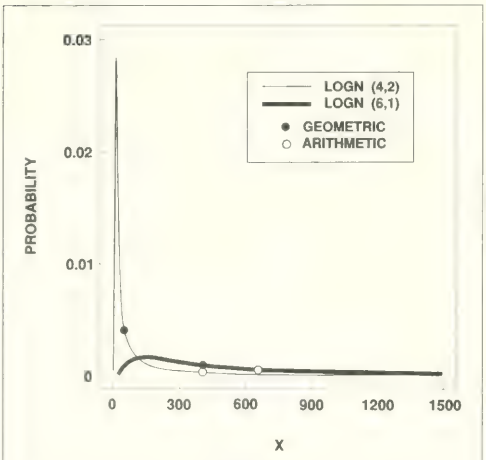

Figure 1

Probability density functions for the representative lognormal distributions. Included are reference marks to indicate values of the respective arithmetic and geometric means.

We investigated three methods of estimating central tendency. The AM method consisted of computing arithmetic means and traditional confidence intervals (e.g., at 90% confidence) based on the Student's t-distribution. The FM method used the Finney-Sichel estimator for the mean of a lognormal distribution as presented in Eq. (1) and (2). For confidence limits, the method by Land (1971, 1975) as presented in Eq. (3) and (4) was used. The GM method used $e^{\bar{Y}}$ as an estimate of $e^{\mu_{LN}}$, the geometric mean (or median) in the untransformed scale. A 90% confidence interval was derived as follows:

$$\exp\left(\bar{Y} - t_{n-1}\frac{S_Y}{\sqrt{n}}\right), \exp\left(\bar{Y} + t_{n-1}\frac{S_Y}{\sqrt{n}}\right). \quad (5)$$

This method estimates a different parameter (the median rather than the population mean) than the first two methods. However, because the median is asymptotically a function of only a single parameter, μ_{LN}, the GM method tends to give more stable estimates of its parameter, and it is worthwhile to compare its performance as another index of central tendency to the first two methods.

Comparison measures to evaluate performance of the estimators

We used the following measures of comparison to evaluate the performance of the estimators: root mean squared error (RMSE), deviation of the estimate from the true parameter (BIAS), average length of the 90% confidence interval (AVL), standard deviation of the 90% confidence interval length (SDCI), and percent containment of the parameter by the confidence interval estimate (PERCON). These were estimated as follows:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{1000} (\textit{estimated parameter from } i^{\text{th}} \textit{ data set} - \textit{true value})^2}{1000}}.$$

Root mean squared error is a measure of the average variation in the estimated mean relative to the true

Table 2a

Descriptive statistics for 1000 simulated trawl data sets representative of **coastal** populations of *Cancer magister* in Washington [Lognormal (4,2)]. Trimmed means calculated using the central 90% of the individual data sets. Min/Max refer to the minimum and maximum values in the data set.

	Arithmetic mean		Trimmed mean		Standard deviation			
n	Raw[a]	Log[b]	Raw	Log	Raw	Log	Min	Max
2	431	4.104	192	4.106	1,949	2.026	<1	48,860
4	382	4.003	163	4.004	1,714	1.999	<1	64,248
6	398	3.987	162	3.988	1.946	2.007	<1	62,131
8	370	3.985	157	3.984	1,818	1.982	<1	71,789
10	386	4.001	161	4.002	1,964	1.996	<1	110,761
15	378	4.002	163	4.007	1,723	2.002	<1	82,492
20	391	4.004	162	4.003	1,920	1.997	<1	122,967
25	394	3.999	159	4.002	2,313	1.991	<1	160,546
30	407	4.002	161	4.004	2,603	2.000	<1	236,341
35	422	4.016	162	4.015	3,301	1.992	<1	380,743
40	419	3.999	161	3.999	7,609	1.997	<1	1,479,353
45	397	3.989	162	3.989	2,167	2.010	<1	226,970
50	411	4.003	163	4.003	2,525	2.008	<1	323,734

True value of μ *is* $403.43 = \exp\left(4 + \frac{2^2}{2}\right)$; *(see Appendix).*

[a] untransformed density (*n*/ha).
[b] log-transformed density (*n*/ha).

Table 2b

Descriptive statistics for 1000 simulated trawl data sets representative of **estuarine** populations of Dungeness crab *Cancer magister* in Washington [Lognormal (6,1)]. Trimmed means calculated using the central 90% of the individual data sets. Min/Max refer to minimum and maximum values in the data set.

	Arithmetic mean		Trimmed mean		Standard deviation			
n	Raw[a]	Log[b]	Raw	Log	Raw	Log	Min	Max
2	633	5.968	528	5.971	739	.994	10	5,703
4	676	6.007	552	6.007	860	1.012	10	10,525
6	682	6.026	557	6.024	924	.993	11	24,259
8	690	6.010	553	6.006	955	1.016	12	20,499
10	659	5.993	541	5.995	835	1.004	6	13,333
15	650	5.986	537	5.986	816	.993	12	18,877
20	655	5.992	538	5.993	825	.998	8	13,756
25	667	6.000	544	5.999	868	1.003	4	19,785
30	664	5.995	543	5.995	857	1.004	5	21,060
35	664	5.999	541	5.998	901	.995	7	30,309
40	657	5.996	540	5.995	844	.993	9	20,555
45	666	6.004	547	6.004	869	.997	6	30,655
50	664	6.001	544	6.002	856	.998	7	18,725

True value of μ *is* $665.14 = \exp\left(6 + \frac{1^2}{2}\right)$; *(see Appendix).*

[a] untransformed density (*n*/ha).
[b] log-transformed density (*n*/ha).

mean density and, as such, is a measure of accuracy. For any unbiased estimator (e.g., the AM or FM, where the expected value of the estimator is the parameter itself), the RMSE is the same as the variance of the estimator, in terms of expected value. For a biased estimate (recall that GM has positive bias in estimating $e^{\mu_{LN}}$, which decreases as n increases), RMSE incorporates both bias and variance.

$$BIAS = \sqrt{\frac{\sum_{i=1}^{1000} (\textit{estimated parameter from } i^{th} \textit{ data set} - \textit{true value})}{1000}}$$

$$= (\textit{average value of estimated parameter} - \textit{true parameter}).$$

The bias is the average amount by which the estimate tends to "miss" its respective parameter.

$$AVL = \frac{\sum_{i=1}^{1000} (UL - LL)_i}{1000} = \frac{\sum_{i=1}^{1000} length_i}{1000},$$

where $(UL–LL)_i$ = length of a single 90% confidence interval for the i^{th} data set. The average length is a measure of precision.

$$SDCI = \sqrt{\frac{\sum_{i=1}^{1000} (length_i - AVL)^2}{1000 - 1}}.$$

The standard deviation is a measure of the spread of the confidence-interval lengths around the average length. An estimator with the most reproducible estimate of the precision of the estimated mean would have confidence intervals of relatively low variability in length.

The frequency with which a confidence interval includes the true value of the parameter defines the containment rate, PERCON. If the assumptions of sampling and the appropriateness of statistical model are met, 90% confidence intervals should contain the density parameter being estimated approximately 90% of the time.

The three estimators of central tendency (AM, FM, GM) and their confidence intervals were also calculated for actual density data obtained during the monthly trawl surveys. Two large systems, termed the Coast and the Estuary, were considered.

Results

Monte Carlo simulations

Root mean squared error The RMSE was consistently lower for the GM than for the other measures of central tendency (Fig. 2). The FM provided point estimates of μ that were consistently more accurate (except at very small sample sizes) than the AM method, particularly as skewness of the density data (Fig. 1) increased. The RMSE of GM estimates and of μ obtained with the FM declined steadily as sample size increased, whereas that for the AM, although generally declining, was somewhat less regular and much more erratic (see Fig. 2a, n=40). Closer inspection of the LOGN (4,2) data set revealed a single extreme

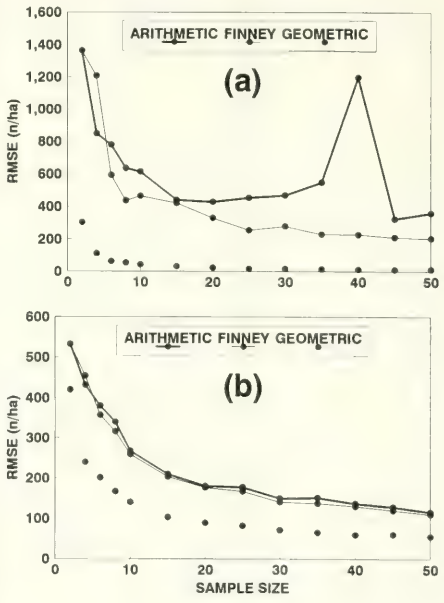

Figure 2

Comparison of root mean-square error (RMSE) values associated with the three estimators of central tendency according to sample size. **(a)** LOGN (4,2) data representative of coastal population of *Cancer magister* used for Monte Carlo simulations. See text for outlier explanation. **(b)** LOGN (6,1) data representative of estuarine population of *C. magister* used for Monte Carlo simulations.

value out of 40,000 data points that caused a considerable increase in the RMSE associated with the AM estimate. It is noteworthy that the magnitude of this simulated density value is in keeping with extreme values observed in the field. Accuracy of GM estimation improved dramatically as skewness increased, in contrast to the FM and AM responses wherein accuracy decreased as skewness increased.

Deviation of the estimator from the parameter (bias) Overall, the most extreme deviations were associated with the smallest sample sizes; this disparity decreased as sample sizes increased (Fig. 3). GM estimates deviated less, stabilized at smaller sample sizes, and, despite the positive bias, converged much more predictably to $e^{\mu_{LN}}$ than did AM and FM in estimating μ. In general, estimates of μ oscillated about the parametric value and converged as sample size increased. The absolute values of the deviations from μ are smaller for the FM than for the AM method in 17 of the 26 cases examined, without an obvious trend related to the skewness of the data. It is noteworthy that estimates of μ obtained with the AM and FM methods are equivalent when n=2.

Average length of the interval estimate The average length of the 1000 90% confidence intervals (CIs) calculated for each sample size was consistently shorter for the GM (which only estimates one parameter) than for the intervals of the AM or FM (Fig. 4). Intervals calculated using the FM method were consistently larger than those for the AM method. Overall, the degree of difference between the three estimators decreased as sample size increased and as skewness decreased. Average lengths were inordinately large at the smallest sample sizes and decreased rapidly thereafter. The average CI length for the GM decreased as skewness increased, in contrast with the behavior of CI lengths for μ.

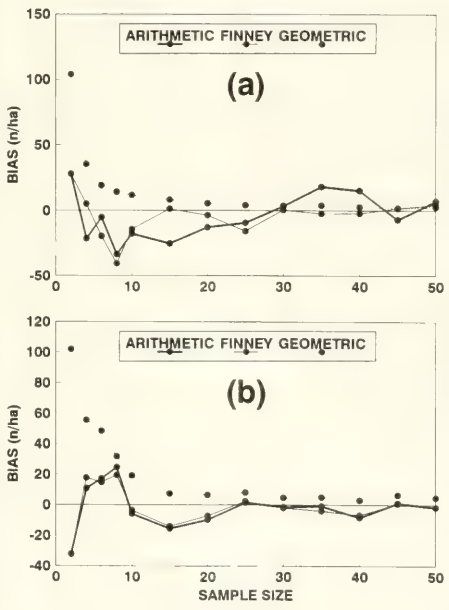

Figure 3

Comparison of degree of deviation from the parameter (bias; scaled to 0) for the three estimators of central tendency according to sample size. **(a)** LOGN (4,2) data representative of coastal population of *Cancer magister* used for Monte Carlo simulations. **(b)** LOGN (6,1) data representative of estuarine population of *C. magister* used for Monte Carlo simulations.

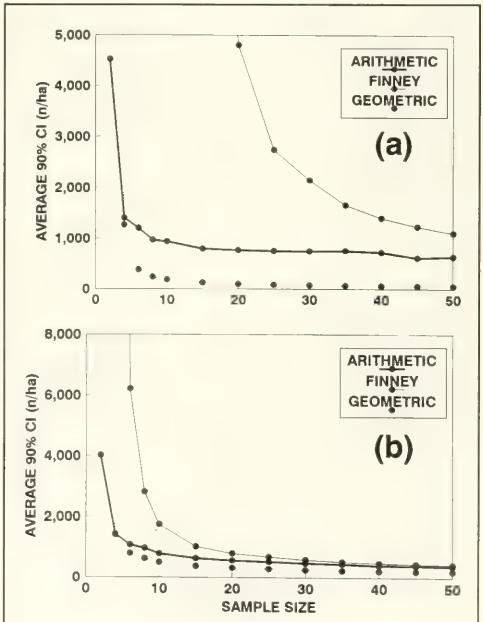

Figure 4

Comparison of average length of 90% confidence interval for the three estimators of central tendency according to sample size. **(a)** LOGN (4,2) data representative of coastal population of *Cancer magister* used for Monte Carlo simulations. **(b)** LOGN (6,1) data representative of estuarine population of *C. magister* used for Monte Carlo simulations.

Standard deviation of the confidence interval length The standard deviation of the 1000 90% CIs calculated for each sample size was consistently lower for the GM than for the AM or FM, both in an absolute sense and relative to the average CI length (Fig. 5). At smaller sample sizes, the standard deviations for the AM were less than those for the FM. However, this pattern was reversed at larger sample sizes such that the FM had the more precise interval estimates (note the crossovers at n=35 and n=25 in Figs. 5a and 5b, respectively). Overall, the precision of the interval estimates declined as sample size decreased and as skewness increased; the effect was most pronounced for the FM method. The GM response was unique in that precision increased as skewness increased. Of particular note is the dramatic loss of precision of the AM interval estimate apparent in Fig. 5a (n=40) which, upon investigation, was attributed to a single extreme value.

Parameter containment within the interval estimate The GM parameter $e^{\mu_{LN}}$ occurred within its interval estimates, as did μ within the intervals obtained by using FM, at the prescribed 90% confidence level (Fig. 6). The rate of GM containment oscillated within 1–2% of this level under all circumstances. Confidence intervals for the FM contained μ at the rates of 89.1–92.3% (Fig. 6a) and 89.1–93.6% (Fig. 6b); the highest percentages were associated with the smallest sample size, perhaps due to their relatively greater lengths (Fig. 5). In contrast, AM interval estimates contained μ at rates of 47.7–65.8% (Fig. 6a) and 76.9–85.3% (Fig. 6b), well below the prescribed level of confidence.

Dungeness crab trawl survey data

We also computed the three estimators for actual *C. magister* density data to assess the gain in informa-

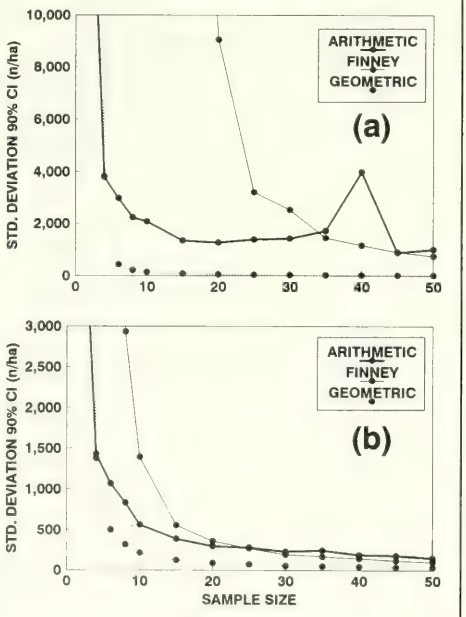

Figure 5

Comparison of standard deviation of the length of 90% confidence interval for the three estimators of central tendency according to sample size. **(a)** LOGN (4,2) data representative of coastal population of *Cancer magister* used for Monte Carlo simulations. **(b)** LOGN (6,1) data representative of estuarine population of *C. magister* used for Monte Carlo simulations.

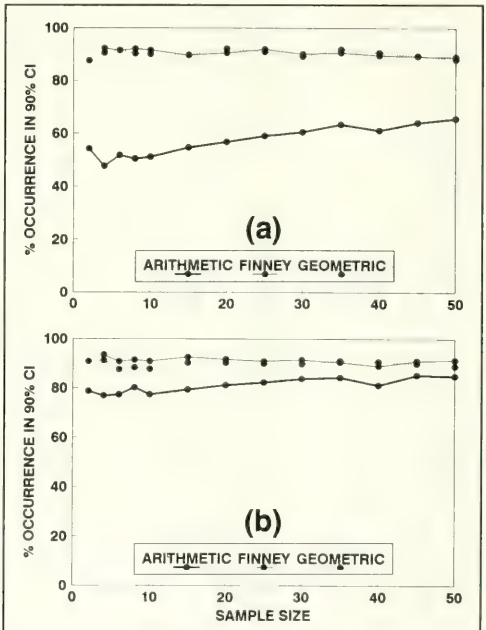

Figure 6

Comparison of percent occurrence of the parameter in the 90% confidence interval for the three estimators of central tendency according to sample size of *Cancer magister*. **(a)** LOGN (4,2) data representative of coastal population of *C. magister* used for Monte Carlo simulations. **(b)** LOGN (6,1) data representative of estuarine population of *C. magister* used for Monte Carlo simulations.

tion over using any single estimator alone. For the Estuary data, trends in abundance routinely paralleled one another, differing only by their relative magnitude (Fig. 7a). Characteristically, estimates of μ from the survey data obtained with the FM method exceeded those of the AM, which, in turn, exceeded estimates of the GM parameter ($e^{\mu_{LN}}$). In some cases, trends in the Coast estimates were diametrically opposed (Fig. 7b). As expected, the GM estimate was consistently lower than both AM and FM, reflecting the difference in the population parameter being estimated. Noteworthy was the reversal in the relative magnitudes of the AM and FM estimates during the interval between Cruise 2 and Cruise 4.

Discussion

Conventional analysis of catch data and alternatives

Population estimates are routinely generated using untransformed catch data and arithmetic mean calculations (e.g., BIOMASS procedure of the U.S. NMFS, Gunderson et al. 1978; STRAP procedure of Can. Dep. Fish. & Oceans, Smith & Somerton 1981). Several methods for reducing the variance associated with these estimates of abundance have been used, often despite recognizable limitations. These fall broadly into two categories: (1) model-based approaches, which model the underlying distribution of the data, and (2) design-based approaches, which rely upon probability sampling and large sample results. Smith (1990) compared the two approaches for estimating resource abundance with trawl surveys and concluded with an example of a model-based predictive estimate using additional information (salinity, temperature, depth). Other examples of model-based estimation in fisheries applications include use of a weighted negative binomial distribution (Zweifel & Smith 1981), the delta distribution (Pennington 1983), and the geostatistical technique of kriging (Conan 1985). Stratification of the sampling frame is a common example of a design-based approach. Although this is theoretically appealing, Gavaris & Smith (1987) have demonstrated that stratified random sampling may be inferior to a simple random design, because of suboptimal allocation of stations to strata. They suggest that a decrease in the number of strata used in the eastern Scotian Shelf groundfish survey would provide for more flexible allocation of total sampling effort in the future. Unfortunately, many of the problems attendant with specifying stratum boundaries will persist; these include interannual variability in distribution and abundance of stocks related to environmental factors and the typical multi-species scope of most research trawl surveys. Because of these difficulties, catch data are commonly stratified *after* sampling is completed (Picquelle & Stauffer 1985, Otto 1986). However, post-stratification (i.e., *a priori* examination of catch data for the purpose of assigning strata) is not a valid approach and is not recommended (Cochran 1977).

Other methods for estimation of abundance are expedient, yet may be based on the specious assumption that extreme values are "outliers" and are therefore not integral to the data set. Included is the practice of eliminating extreme values or the use of trimmed (or Winsorized) means (Halliday & Koeller 1981, Bates 1987, Harding et al. 1987, Smith 1981). Ignoring instances where human error is involved, these *ad hoc* procedures may introduce substantial negative bias to estimates of the true population mean (compare μ and the trimmed means in Table 2), thereby contributing to misleading conclusions about trends in the data.

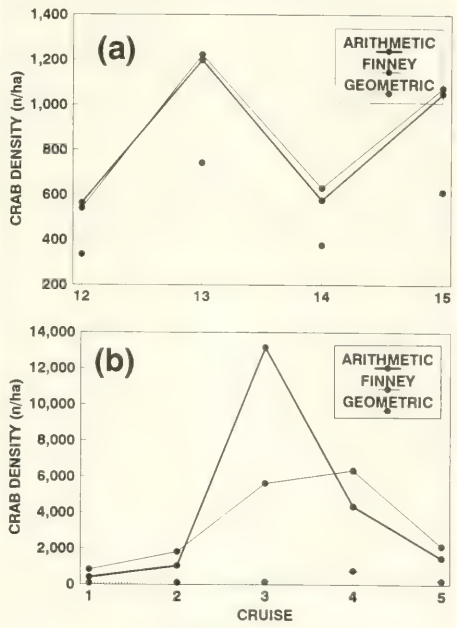

Figure 7

Comparison of three measures of central tendency calculated for *Cancer magister* using monthly cruise data for **(a)** the estuarine area (year 3) and **(b)** the coastal area (year 1). (The order of the coast/estuary figures is deliberately reversed here to illustrate certain results; see text.)

Design-based and model-based approaches

A strict probability sampling approach (i.e., design-based and without any underlying models) requires

that resulting estimates be normally distributed according to the Central Limit Theorem. However, Hansen et al. (1983) state, "When surveys use relatively small samples, the samples may be too small for the application of the theory [for large samples] to be essentially assumption-free." Our approach is model-based. As long as one is restricted to samples that may not be considered "acceptably large" (and further hampered by considerable skewness caused by extreme values), use of a model-based approach is not unwarranted (Little 1983).

With regard to robustness, Myers & Pepin (1990) argue that exclusive use of a lognormally-based estimate can be sensitive to model assumptions, leading to possible bias and reduction in efficiency. Because contamination of a lognormal distribution with data from similarly-shaped distributions (e.g., Weibull or gamma) is difficult to detect for sample sizes less than 40, they suggest using lognormally-based estimators of abundance only when there is evidence that the underlying population is lognormal. Obviously, use of transformations and model-based estimators is a "double-edged sword," and these procedures should not be applied indiscriminately. When appropriate (e.g., Table 1), however, significant improvement in the relative efficiency of the sample average and, in particular, the estimated variance, can be realized (e.g., Finney 1941, Koch & Link 1970, Myers & Pepin 1990).

A comparative approach

If nothing is known about the spatial distribution of an organism, the sampling plan must be designed to determine distribution patterns as well as population size. Knowledge of the distribution pattern aids in selection of the proper estimation procedure. Based on the arguments presented above, combined with the rather ubiquitous nature of overdispersion in the marine environment, we prefer an approach based on three estimators, namely the arithmetic mean, the geometric mean, and the Finney-Sichel estimator of μ. By taking a comparative approach, one may be reasonably certain of apparent trends in the data if the trend is consistent for the three estimators. For the estuarine crab population illustrated in Figure 7a, the parallel behavior of the estimates corresponded to changing values of $\bar{Y}$ coupled with nominal changes in s^2_Y (Table 1). In this case, there is no evidence to suggest that conventional analysis of catch data (i.e., using the AM method) was less than adequate. However, trends in the estimates may, on occasion, be opposed to one another, as was demonstrated for the coastal crab population (Fig. 7b). The AMs suggest a precipitous drop in abundance occurred during the interval between Cruises 3 (with two extreme values) and 4, whereas both the FM and GM procedures indicated a moderate increasing trend during the same period. From the behavior of the three estimators, we conclude that between Cruises 2 and 4, μ_{LN} (and μ) may have increased slightly, but σ^2_{LN} (and thus the skewness of the distribution) probably increased and then decreased, affecting the FM and AM estimates (the latter more strongly) but not the GM estimate. This is verified by checking the $\bar{Y}$ and s^2_Y values in Table 1. Changes in skewness relate directly to the size of the larger catches and, hence, the degree of spatial aggregation in the population. Plotting the three estimators and relating the trends back to changes in $\bar{Y}$ and changing s^2_Y has yielded some insight into the behavior of the estimators. It has also allowed us to extract more information about the crab population than if we had used only one estimator, the AM. In cases such as this, where there is significant disagreement among the estimators, the data set should be carefully evaluated as to its underlying probability distribution and the most appropriate index selected. If the lognormal distribution is reasonable, the GM may well be the preferred estimator (Aitchison & Brown 1969); use of the GM may be advantageous because it is relatively insensitive to extreme values (particularly so for highly-skewed data) in terms of accuracy and precision. Since catch coefficients are not routinely considered with trawl-survey data of this type, the resulting stock-size estimates are, strictly speaking, *indices* of abundance (Caddy 1986). Under these circumstances, it may be advantageous to use an alternative estimator of central tendency, such as the GM, to generate the index.

Acknowledgments

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Appendix

A random variable X is considered to be lognormally distributed when the natural logarithm of X, Y=ln(X), has a normal distribution. Specifically, if Y is normally distributed with mean μ_{LN} and standard deviation σ_{LN}, then $X=e^Y$ is lognormally distributed with density function (Aitchison & Brown 1969):

$$f(X) = \frac{1}{\sqrt{2\pi}\,\sigma_{LN}X} \exp\left(\frac{-(\ln X - \mu_{LN})^2}{2\sigma^2_{LN}}\right). \quad \text{(A1)}$$

The kth moment about zero, $E(X^k)$ is expressed as

$$E(X^k) = E\,(e^{kY}) = \exp\left(k\mu_{LN} + \frac{\sigma_{LN}k^2}{2}\right). \quad \text{(A2)}$$

In particular,

$$\textit{Population Mean} = \mu = \exp\left(\mu_{LN} + \frac{\sigma^2_{LN}}{2}\right), \quad \text{(A3)}$$

$$\textit{Variance (X)} = \sigma^2 = [\exp(\sigma^2_{LN}) - 1] \cdot [\exp(2\mu_{LN} + \sigma^2_{LN})], \quad \text{(A4)}$$

$$\textit{Geometric Mean} = \textit{Median (X)} = \exp(\mu_{LN}). \quad \text{(A5)}$$

Abstract.—Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus* expressed significant differences in their early-life-history traits under laboratory conditions. Eggs of Atlantic menhaden were larger and contained more yolk. Their larvae were larger at hatching, and contained more yolk. A suite of developmental events (yolk depletion, age at first feeding, and, possibly, age at metamorphosis) was achieved earlier in Atlantic menhaden. The expression of these early-life-history traits in each species may reflect adaptations to the contrasting environments that these species occupy.

A comparison of early-life-history traits in Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus*

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Progeny size is a key life-history trait that has evolved in response to the predictability of the reproductive environment (Stearns 1976). The influence of progeny size on early-life-history characteristics has received considerable attention (Blaxter & Hempel 1963; see reviews or summaries by Miller et al. 1988, Hinckley 1990, Pepin 1991); however, comparative early-life-history studies between congeners are sparse and largely restricted to salmonids (e.g., Beacham & Murray 1990). A preliminary study suggested differences between early life histories of the Atlantic and gulf menhadens (Powell & Phonlor 1986). Here, a more extended and detailed documentation of differences between these menhadens is provided.

Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus* are morphologically-similar allopatric clupeids. Both are schooling, filter-feeding clupeids that use estuaries during their first year of life. Individuals of Atlantic menhaden range from Nova Scotia to Florida and thus encounter variable environmental conditions during their lifetime. The distribution of Atlantic menhaden is stratified by age and size, with older and larger fish ranging further north (Nicholson 1971). Spawning is protracted and occurs throughout its range, in inshore waters during summer and early fall in Long Island Sound and New England. From Long Island to Chesapeake Bay, spawning occurs offshore during October–December and March–May (Higham & Nicholson 1964).

Gulf menhaden, in contrast, are restricted to the Gulf of Mexico, distributed from Cape Sable, FL to Vera Cruz, Mexico (Reintjes 1969). Spawning occurs October through March in nearshore and offshore coastal waters (Christmas & Waller 1975).

The specific objective of this study was an interspecific comparison of egg size, yolk volume, and the characteristics they may influence: size-at-hatching, first-feeding and metamorphosis, resistance to starvation, development (yolk and oil depletion, age-at-first-feeding), growth, and mouth size. In addition, for Atlantic menhaden, relationship between egg size and latitude of capture was evaluated.

Methods and materials

Spawning and rearing

Adult gulf menhaden (179–201 mmTL) were captured by cast net in Pensacola Bay, FL in the fall of 1983–85 and transported to Beaufort, NC (methods followed Hettler 1983). Adult Atlantic menhaden (204–212 mmTL) were collected from commercial purse seines in Core Sound,

NC in the summers of 1983 and 1985. Menhaden were held at the laboratory in Beaufort at ambient temperatures until water temperatures fell below 20°C. Thereafter, temperatures were maintained at ca. 20°C. Ten menhaden were induced to spawn at each spawning (methods followed Hettler 1981, 1983). Generally, spawning occurred in 20°C water at night, and eggs were collected in the morning. Eggs were held either in 10 L black-sided tanks with static water immersed in a temperature-controlled water bath or in 100 L black-sided rearing tanks with static water. Temperatures in the 100 L tanks varied with slight changes in room temperature (19–20°C). Salinities ranged from approximately 30 to 35‰. Two 40 W fluorescent lamps were placed 90 cm above each large rearing tank and 40 cm above each small tank. The tanks were illuminated for a 12 h dark:12 h light cycle. Rotifers *Brachionus plicatilis* were the sole source of food. Experimental temperatures were 16°, 20°, and 24°C. These temperatures were chosen because 20°C approximates the average temperature of most intensive spawning for both species (Shaw et al. 1985, Checkley et al. 1988). The 16° and 24°C temperatures were arbitrarily chosen to bracket the 20°C temperature and were in accord with a previous study (Powell & Phonlor 1986).

Eggs

Egg, yolk, and oil globule diameters were measured on approximately 50 live eggs per spawning for each species. Yolk and oil diameters were used to calculate volumes. Because the spheroidal oil globule is embedded in the prolate spheroidal yolk mass, oil volumes were subtracted from initial yolk volume estimates to give a more accurate measurement of yolk volume.

Relationship between egg size and latitude was investigated by using collections of preserved (5% formalin) Atlantic menhaden eggs from eight cruises during 1979–81 by the Sandy Hook Laboratory, NMFS Northeast Fisheries Science Center, Highlands, NJ.

Larvae

Starvation experiments were conducted at 16°, 20°, and 24°C. Approximately 20–25 larvae were removed from the rearing tanks and randomly placed in each 1L fingerbowl at each experimental temperature on the day prior to initiation of feeding by the larvae. Food was withheld from all larvae. Mortalities were recorded at 24 h intervals. Results from repeated independent experiments (n=6 and 3 for Atlantic and gulf menhaden, respectively) were averaged.

Mean standard lengths (SL) and mean dry weights of menhaden larvae at hatching and at first-feeding were determined from larvae reared at 16°, 20°, and 24°C in 10 L tanks. Mean lengths and mean dry weights were obtained from approximately 10 preserved larvae (5% buffered formalin) per experiment. To determine when first-feeding occurred, 10 larvae at each experimental temperature were removed daily, preserved, and inspected for the presence or absence of rotifers. The presence of rotifers in the guts of any of the 10 larvae was considered to be first-feeding. Observations on development were also made (e.g., fully-pigmented eyes, functional mouth, and differentiated foregut and midgut). All observations were made at 50× magnification.

Mean rate of yolk absorption was determined from approximately 10 larvae sampled daily at 16°, 20°, and 24°C, from time of hatching until the time when yolk and oil were completely used. Because preservation had a significant effect (P<0.01, n=50) on size and condition of the yolksac (preserved yolk diameters were smaller than those measured live), measurements were made only on live material. Yolk volumes were calculated using the formula for a prolate spheroid,

$$V = (\pi/6)\, l\, h^2,$$

where l is length and h is the height of the yolk mass (Blaxter & Hempel 1963). As with the measurement of eggs, oil volumes were calculated and subtracted from the calculated yolk volumes to give a better estimate of yolk volume.

Two series of growth experiments were conducted on each species. One examined the relationship between growth and survival of menhaden larvae in relation to temperature and food density. Groups of 50 larvae, approximately 6 d old, were removed from 100 L rearing tanks and transferred to each 10 L experimental tank. The larvae were slowly acclimated (~4 h) to 16°, 20°, or 24°C. Food levels were designed to reflect high, moderate, and low food availabilities. Food levels the first year (1984) were 50, 25, and 5 rotifers/mL, and two replicates were performed at each food level for each species. These food levels did not limit growth. Food levels of 10.0, 1.0, 0.1, and 0.025 rotifers/mL were employed the following years (1985 and 1986) and three replicates were performed. Over the course of a 7 d experiment, food densities were monitored daily and adjusted on the basis of the average of three samples from each rearing tank. Growth was determined as the difference between mean size of the preserved survivors at the end of the experiment and mean size of 50 preserved larvae removed from the 100 L tank at the beginning of the experiment. Larvae for each tank were combined, dry weights obtained, and values expressed as mean dry weight. The gain in biomass over a 7 d period was calculated to weight the number of

survivors, which varied markedly. Growth and survival between species were compared using this index.

Gain in biomass (B) for each tank was calculated as

$$B = (W_t - W_{t\ 7})(S),$$

where W = mean dry weight/fish, t = age in days, and S = number of survivors.

A second series of growth experiments was conducted to examine instantaneous daily growth rates and size of larvae 10 d past first-feeding. Eggs and larvae were reared in 10 L tanks at 16°, 20°, and 24°C. Larvae were maintained on high food densities (~ >25 rotifers/mL). For each experimental temperature, 10 larvae were sampled 10 d past first-feeding. Length (SL), dry weight, and mouth width (an estimate of gape size) were obtained from preserved larvae. Daily instantaneous rates of increase in length and weight were calculated according to Ricker (1975:207).

Length-weight relationships were used to estimate sizes separating early-life-history periods (Balon 1984). Larvae were measured live, and dry weights were obtained from larvae that were preserved by freezing. For each species, an iterative process was used to determine the break point (SL) between two regressions that described the length/weight relationship. Iterations were done with break point values of 8–14 mmSL at 1 mm intervals. The two regressions that resulted in the minimal mean square error were chosen. An ANCOVA was used to compare the biphasic regressions.

Statistical testing was done by using the General Linear Model procedure (SAS 1985). Unless otherwise noted, ANOVA was used to test differences. Each treatment consisted of a group of larvae in a common tank. The mean measurement (e.g., mean length or mean weight of the group) was used in the statistical analysis. Each experiental replicate was treated as an independent observation. Differences between main effects were considered significant at α=0.05. For interaction between factors, differences were considered significant at α=0.10 to reduce the chance of a type-II error.

Results

Atlantic menhaden eggs were larger in diameter and nearly two-fold heavier than gulf menhaden eggs (Table 1, 2). The volume of yolk was greater for Atlantic menhaden, but oil globule volumes were similar (Table 1, 2).

There was no discernible change in egg size during the laboratory spawning season (Fig. 1), and the level of variability throughout the season was smaller for gulf (SD=0.02–0.04) than Atlantic (SD=0.04–08) menhaden. There was a trend for field-collected Atlantic menhaden eggs to be larger at higher latitudes (P<0.01), but there was a considerable amount of variability in egg size for any given latitude (Fig. 2).

Newly-hatched, laboratory-reared Atlantic menhaden were longer and heavier than gulf menhaden (Table 1, 3). Temperature affected length-at-hatching, in that larvae (especially gulf menhaden larvae) were longer

Table 1

Summary of analysis of variance results expressed as P-values (Pr>F) for gulf and Atlantic menhaden. S = species, T = temperatures, S×T = species × temperature interactions, F = food, S×F = species × food interaction, T×F = temperature × food interaction, and S×F×T = species × food × temperature interaction.

Factor	Class		
	S	T	S×T
Egg diameter	<0.01		
Egg yolk volume	0.01		
Egg oil volume	0.24		
Size at hatching	<0.01	0.01	0.51
Weight at hatching	<0.01	0.08	0.65
Yolk volume at hatching	<0.01	0.14	0.62
Oil volume at hatching	0.01	0.94	0.83
Yolk utilization rate	<0.01	<0.01	0.14
Oil utilization rate	0.33	<0.01	0.12
Yolk volume at first-feeding	0.80	0.87	0.80
Oil volume at first-feeding	0.23	0.22	0.44
Age at first-feeding	<0.01	<0.01	0.32
Length at first-feeding	0.00	0.24	0.77
Weight at first-feeding	0.19	0.51	0.26
Growth rate (10 d) in length	0.53	0.03	0.07
Growth rate (10 d) in weight	0.03	0.06	0.08
Length 10 d past first-feeding	<0.01	0.16	0.06
Weight 10 d past first-feeding	<0.01	0.01	0.03
Mouth gape 10 d past first-feeding	0.90	0.02	0.13

	S	T	S×T	F	S×F	T×F	S×T×F
Growth in biomass	0.79	<0.01	0.97	<0.01	0.99	0.10	0.97

Table 2

Summary of Atlantic and gulf menhaden egg data. Values in parentheses indicate the number of replicates. For each experiment ~50 eggs were measured or weighed.

Species	Eggs		Yolk	Oil Globule
	Mean diameter (mm±SD)	Mean dry weight (µg)	Mean volume (mm^3±SD)	Mean volume (mm^3±SD)
Atlantic menhaden	1.61±0.08 (9)	78 (2)	0.583±0.0561 (6)	0.003±0.0006 (6)
Gulf menhaden	1.22±0.04 (7)	43 (2)	0.483±0.0359 (4)	0.003±0.0003 (4)

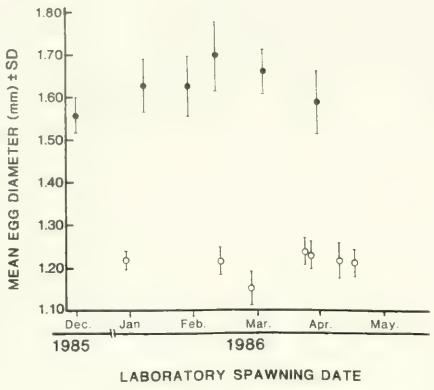

Figure 1

Relationship between mean egg size and laboratory spawning date for *Brevoortia tyrannus* (●) and *B. patronus* (○). Observations ($\bar{x}$±SD) are derived from approximately 50 eggs.

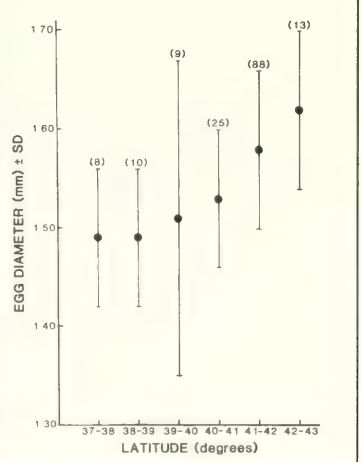

Figure 2

Relationship between egg size ($\bar{x}$±SD) and latitude of capture for *Brevoortia tyrannus*. Numbers in parentheses indicate number of eggs measured.

at lower incubation temperatures. On the other hand, incubation temperatures in the laboratory did not affect the weight of larvae at hatching (Table 1, 3).

Yolk reserves were larger for Atlantic menhaden at hatching, but oil reserves were greater for gulf menhaden (Table 1, 3). Temperature did not affect the amount of oil or yolk reserves for recently-hatched Atlantic or gulf menhadens. After hatching, both species utilized yolk and oil reserves at an exponential rate (Table 4). Atlantic menhaden utilized yolk reserves at a higher rate than gulf menhaden, but rates of oil depletion did not differ (Table 1, 4). Temperature affected rates of yolk and oil utilization. At first-feeding, the oil globule and yolk were virtually depleted (Table 3). Yolk reserves at this time were similar for the two species and were independent of rearing temperature. The age at which anatomical features associated with first-feeding appeared (eye pigment, fore- and midgut, and functional mouth) did not differ, but the interval between the appearance of these features and first-feeding was shorter for Atlantic menhaden (Table 5).

At first-feeding, Atlantic menhaden were significantly longer and younger than, but of similar weight to, gulf menhaden (Table 1, 3). Although length-at-hatching increased with decreasing temperature, temperature did not influence length of larvae at first-feeding. Age-at-first-feeding decreased with increasing temperatures for both species (Table 1, 3).

First-feeding Atlantic menhaden, which are longer than first-feeding gulf menhaden, may be slightly more resistant to starvation (Fig. 3). Atlantic menhaden lived 1–2 d longer than gulf menhaden. The survivorship curves of the two species were similarly shaped at the same temperature. At the highest temperature (24°C) survivorship declined rapidly after the third day, while at the lowest temperature (16°C) it was nearly linear with time.

The amount of biomass gained during the early stages did not differ between species (Table 1, Fig. 4). Population biomass of both menhadens was relatively low at 16°C, as compared with 20°C and 24°C when food was not limiting. Food concentrations of ≤1.0 rotifer/mL similarly limited the growth and survival of both species. Low temperature (i.e., 16°C) affected biomass gained by larvae of both species during this 7 d feeding and growth study.

Interactions between species and temperature were observed for all growth experiments (Table 1, Fig. 4). Atlantic menhaden growth was lower at 16°C than at 20° and 24°C. Gulf menhaden growth did not appear to differ between temperatures. Atlantic menhaden exhibited higher growth rates at 20° and 24°C, and, in like manner, were larger than gulf menhaden 10 d past first-feeding; however, mouth gape at this time did not differ between species (Table 1, 3).

Atlantic menhaden may attain its size-threshold for metamorphosis (i.e., Balon's 1984 concept) earlier than gulf menhaden (Figs. 5, 6). Length-weight relationships expressed during early-

Table 3

Summary of data ($\bar{x}\pm$SD) for larval Atlantic and gulf menhaden. Values for specific temperatures are given only when temperature had a statistically-significant (α=0.05) influence on the trait. An asterisk (*) preceding the trait indicates a statistically-significant (α=0.05) difference between species. Values in parentheses indicate the number of replicates. Means are calculated from replicate means.

Trait	Temperature (°C)	Atlantic menhaden	Gulf menhaden
*Size at hatching (mmSL)	16	3.4 ± 0.2 (4)	3.1 ± 0.2 (4)
	20	3.2 ± 0.2 (4)	2.6 ± 0.1 (4)
	24	3.2 ± 0.1 (3)	2.8 ± 0.2 (4)
*Dry weight at hatching (μg)	—	49.8 ± 5.0 (11)	39.3 ± 5.9 (12)
*Yolk volume at hatching (mm^3)	—	0.1512 ± 0.0220 (15)	0.1205 ± 0.0259 (11)
*Oil volume at hatching (mm^3)	—	0.0023 ± 0.0005 (15)	0.0029 ± 0.0004 (11)
Yolk volume at first-feeding (mm^3)	—	0.0002 ± 0.0000 (15)	0.0002 ± 0.0000 (11)
Oil volume at first-feeding (mm^3)	—	0.00 (15)	0.00 (11)
*Age at first-feeding (d)	16	5.2 ± 0.4 (8)	5.7 ± 0.1 (6)
	20	3.0 ± 0.3 (8)	3.9 ± 0.1 (7)
	24	2.4 ± 0.3 (8)	2.9 ± 0.1 (7)
*Size at first-feeding (mmSL)	—	4.8 ± 0.2 (9)	4.3 ± 0.3 (10)
Dry weight at first-feeding (μg)	—	37.8 ± 2.6 (9)	35.1 ± 1.6 (10)
Growth rate (10 d) in length (ln mm/d)**	16	0.027 ± 0.010 (3)	0.038 ± 0.013 (3)
	20	0.047 ± 0.000 (3)	0.037 ± 0.005 (3)
	24	0.049 ± 0.006 (3)	0.042 ± 0.004 (3)
*Growth rate (10 d) in weight (ln mg/d)**	16	0.051 ± 0.029 (3)	0.061 ± 0.029 (3)
	20	0.103 ± 0.016 (3)	0.062 ± 0.013 (3)
	24	0.102 ± 0.013 (3)	0.062 ± 0.005 (3)
*Length 10 d past first-feeding (mmSL)**	16	6.6 ± 0.7 (3)	6.5 ± 0.8 (3)
	20	7.9 ± 0.1 (3)	6.2 ± 0.3 (3)
	24	7.7 ± 0.0 (3)	6.4 ± 0.3 (3)
*Dry Weight 10 d past first-feeding (μg)**	16	62.0 ± 19.2 (3)	60.3 ± 15.8 (3)
	20	115.3 ± 19.6 (3)	63.3 ± 8.1 (3)
	24	100.7 ± 13.4 (3)	71.0 ± 3.5 (3)
Mouth gape 10 d past first-feeding (mm)	16	0.3 ± 0.02 (3)	0.3 ± 0.01 (3)
	20	0.3 ± 0.01 (3)	0.3 ± 0.01 (3)
	24	0.3 ± 0.02 (3)	0.3 ± 0.03 (3)

**A species × temperature interaction was observed.

Table 4

Linear regression equations ($Y=B_0+B_1X_1$) between log$_e$ yolk and oil volume in mm^3 (Y) and age in days (X_1) for gulf and Atlantic menhaden. N = number of replicates.

Species	°C	N	Slope (B_1)	Intercept (B_0)	r^2
Yolk					
Gulf menhaden	16	4	–1.220	–2.089	0.96
	20	4	–1.734	–1.733	0.97
	24	4	–2.228	–2.118	0.98
Atlantic menhaden	16	5	–1.270	–1.765	0.97
	20	5	–2.065	–1.712	0.96
	24	5	–2.595	–1.723	0.97
Oil					
Gulf menhaden	16	4	–1.432	–5.082	0.81
	20	4	–1.819	–4.985	0.86
	24	4	–2.834	–4.814	0.81
Atlantic menhaden	16	5	–1.222	–5.392	0.92
	20	5	–2.041	–5.232	0.83
	24	5	–2.017	–5.714	0.84

Table 5

The mean time (d) before first-feeding when ≥80% of gulf and Atlantic menhaden larvae attained eye pigment (EYE), fore-and midgut (FG/MG), and a functional mouth (MOUTH) in relation to temperature. Values are the means of three replicates. Values in parentheses indicate average age (days post-hatch).

	16°C			20°C			24°C		
Species	FG/MG	Eye	Mouth	FG/MG	Eye	Mouth	FG/MG	Eye	Mouth
Gulf menhaden	1.0 (4.7)	1.3 (4.4)	1.3 (4.4)	0.7 (3.2)	0.7 (3.2)	0.7 (3.2)	0.3 (2.6)	0.3 (2.6)	0.7 (2.2)
Atlantic menhaden	0.3 (4.9)	0.7 (4.5)	0.7 (4.5)	0.3 (2.9)	0.3 (2.9)	0.3 (2.9)	0 (2.4)	0 (2.4)	0 (2.4)

life-history stages of these two menhadens suggest that Atlantic menhaden reaches a size-threshold at a smaller size than gulf menhaden. For regression lines that described the length-weight relationship for Atlantic menhaden >10 mmSL and gulf menhaden >12 mmSL, there were no differences between slopes or intercepts. For Atlantic menhaden ≤10 mmSL and gulf menhaden ≤12 mmSL, there were no differences in slopes between the two species, although their intercepts differed. Beginning at the size-threshold in both species (>10 mmSL for Atlantic menhaden, >12 mmSL for gulf menhaden), there is a larger change in weight in relation to a given change in length, reflecting morphogenic changes.

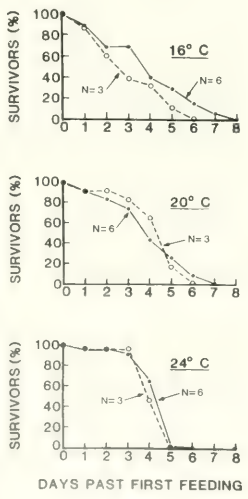

Figure 3

Time to starvation of unfed *Brevoortia tyrannus* (●) and *B. patronus* (○) in relation to temperature. Approximately 25 larvae were used at each experimental temperature. N denotes number of replicates.

Discussion

Egg size and its influence on early-life-history characteristics have received considerable attention. My results, in general, are in accord with other studies of diverse fishes and other organisms. Larger eggs are positively correlated with size of larvae at hatching, yolk reserves, resistance to starvation, and size-at-first-feeding, e.g., Blaxter & Hempel 1963 (clupeoid stocks), Crump 1984 (amphibia), Wallace & Aasjord 1984 (salmonids), Knutsen &

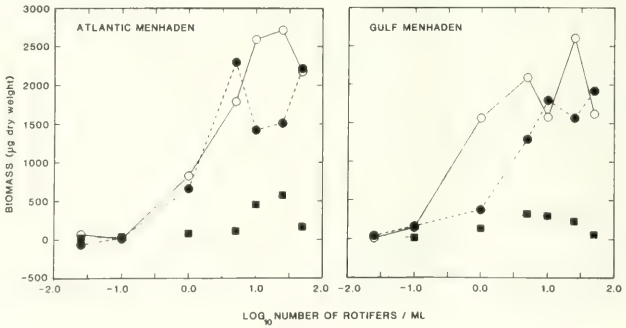

Figure 4

Amount of biomass gained (mean dry weight gained/larvae × number of survivors) over a 7 d period for early-larval *Brevoortia tyrannus* and *B. patronus* at 16 (■), 20 (●) and 24°C (○). Values are means of two replicates for food levels of 5, 25, and 50 rotifers/mL and means of three replicates for all other food levels.

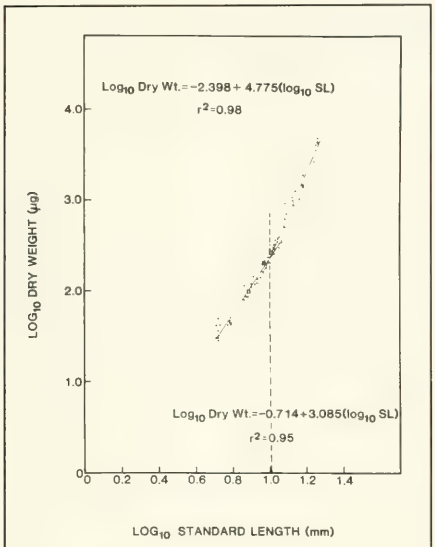

Figure 5
Length-weight relationship of larval *Brevoortia tyrannus* showing a change in body morphology. Breakpoint occurs at 10 mmSL.

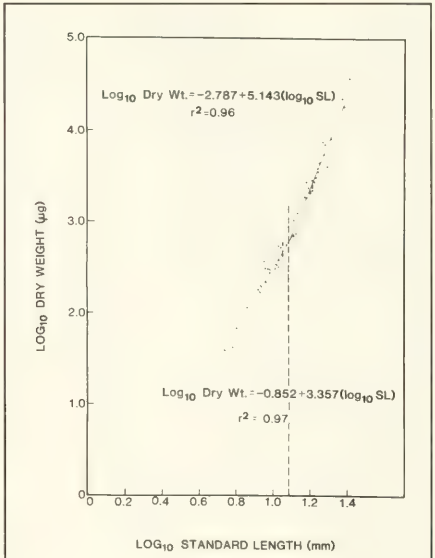

Figure 6
Length-weight relationship of larval *Brevoortia patronus* showing a change in body morphology. Breakpoint occurs at 12 mmSL.

Tilseth 1985 (gadoids), Marsh 1986 (percids), and Goulden et al. 1987 (cladocerans). Relatively larger larvae have been reported to have increased mobility, enhanced encounter rates with prey, and, because of these features, should be better able to detect food (Miller et al. 1988). Large eggs, then, would appear to be more fit in environments where the food supply is relatively poor or variable (Hempel & Blaxter 1967, Goulden et al. 1987). This suggests that the Atlantic menhaden is responding to a more variable or unpredictable reproductive environment than its congener. Because larger eggs appear to confer an advantage over smaller eggs, early survival of larvae from larger eggs should be less variable (Miller et al. 1988). This was not apparent in this study. Although growth rate of early Atlantic menhaden was greater than gulf menhaden at moderate to high temperatures (Table 2), the gain in population biomass of larvae did not differ between species (Table 1, Fig. 4). Pepin (1991) also was unable to support the prediction that larval survival is less variable for species that spawn large eggs.

The cumulative effects of egg size through the early-larval stage may influence menhaden stage duration. Atlantic menhaden not only produce larger eggs and larger larvae at the onset of feeding than do gulf menhaden, but they also have higher rates of yolk utilization and, apparently, higher rates of development (i.e., digestive and sensory systems). Hence, Atlantic menhaden larvae are not only larger, but also younger, than gulf menhaden at first-feeding. This could result in larger larval size shortly after first-feeding (e.g., 10 d), if larvae encounter suitable prey and temperatures. Moreover, Atlantic menhaden appear to undergo transformation of development (based on the relationship between length and weight) at a relatively smaller size, thus spending relatively less time in the early-larval stage. Chambers et al. (1988) showed that winter flounder *Psuedopleuronectes americanus* larvae that metamorphosed early were growing faster than their cohorts despite their small size at metamorphosis. Furthermore, the size advantage acquired during the larval period was maintained during the early-juvenile period. Williams (1966) argued that acceleration of development will occur in those developmental stages in which mortality rates are high. Comparatively, Atlantic menhaden reproduce in an environment that is unpredictable, and the suite of traits exhibited by this menhaden species mediates the unpredictability of the

environment. Further, Atlantic menhaden spawn over a wide range of locations throughout most of the year. This may minimize reproductive failure, because the effects of extreme environmental conditions in one place or time will be dampened by less-extreme environmental conditions in others (Den Boer 1968).

Differences in life-history characteristics between Atlantic and gulf menhadens observed in this study generally are in agreement with previous studies. Reported egg sizes support the observation that Atlantic menhaden eggs are larger than gulf menhaden eggs (Hettler 1984, Powell & Phonlor 1986). The influence of temperature on early-life-history characteristics, interspecific differences in size-at-hatching, and size- and age-at-first-feeding are in accord with findings of Powell & Phonlor (1986). An exception was interspecific differences in growth rate, which were found to differ between species in this study. Interspecific differences between the two menhadens in the wild have been reported by Maillet & Checkley (1991). Although Powell & Phonlor (1986) found no differences in growth rates between species (growth rates were determined at 20°C only), they found a difference in size at age 21 d past first-feeding (Atlantic menhaden 10.7 mmSL, gulf menhaden 8.9 mmSL). This supports observations in the present study that age- and size-at-first-feeding are subtle but important early-life-history characteristics that can influence future size if larvae encounter suitable prey and temperatures.

The influence of temperature on hatching size, as observed in this study, has been linked to larval survivorship. Buckley et al. (1990) reported that recently-hatched and first-feeding winter flounder *Psuedopleuronectes americanus* larvae were longer and displayed greater amounts of protein and nucleic acids at low temperatures, thus maximizing size and condition during the cold winter spawning period. Bengston et al. (1987) observed that recently-hatched Atlantic silverside *Menidia menidia* were larger at low temperatures. They suggested that this conferred a survival advantage to larvae hatched early in the season (colder temperatures), because they are larger at any given age than those hatched later in the season (warmer temperatures). I was unable to detect a survival advantage in this study. Although gulf and Atlantic menhaden were relatively larger at low incubation temperatures (Table 3), incubation temperatures had no influence on size-at-first-feeding.

Certain early-life-history characteristics do not appear to be correlated with egg size. Egg oil volume, oil utilization rates, oil volume at hatching, and weight-at-first-feeding were not related to egg size (Tables 1–3). Egg oil volume has been correlated with resistance to starvation (Chambers et al. 1989). In the present study, there were no differences between menhadens in egg oil volume, and recently-hatched gulf menhaden larvae had a greater volume of oil than Atlantic menhaden, yet still appeared to be least resistant to starvation. This is not surprising, since oil was depleted in both species at first feeding.

A major constraint of this study, and in comparison with previous studies (Hettler 1984, Powell & Phonlor 1986), is that adults from all studies were collected from similar areas and may not be representative of the entire population. Intraspecific latitudinal variation in field-collected Atlantic menhaden egg size has been observed in this study, and variation in egg size has been reported for gulf menhaden (Hettler 1984). Evidence in both studies shows that egg size is related to fish size. Hettler (1984) found that larger laboratory-spawned gulf menhaden (20 cm mean length) produced larger eggs than smaller gulf menhaden (18 cm mean length). Because Atlantic menhaden are distributed by size and age, differences in egg size with latitude might be related to female size. If so, values for the early-life-history variables (e.g., egg size, size-at-hatching, etc.), especially for Atlantic menhaden as reported here, should be viewed with caution because intraspecific and latitudinal variation in life-history variables was not evaluated in this study.

With the exception of salmonids, there are few studies that relate interspecific differences in early-life-history traits to the environments that the species occupy. Beacham & Murray (1990) clearly related variation of early-life-history traits of five species of Pacific salmon to their different spawning environments. As in the present study, alevin and fry weight were greatly influenced by egg size. Given the constraints and limitations of the present study, the differences in egg size which influenced larval size, along with differences in a suite of developmental events observed between the two menhadens, may reflect life-history selection processes that have occurred in their different environments.

Acknowledgments

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Abstract.—Observers from the National Marine Fisheries Service collected information on catch rates of shrimp aboard commercial shrimp vessels during March 1988–August 1990. Comparisons were made between nets equipped with Turtle Excluder Devices (TEDs) and standard shrimp nets. Three types of TEDs were tested: Georgia TEDs with and without accelerator funnels, and Super Shooter TEDs with funnels.

Fishing areas, time of day, and duration of tows were controlled by the captain of each vessel to simulate commercial conditions. A statistically-significant ($P<0.05$) mean loss in shrimp catch-per-unit-effort (CPUE) of 0.24 lb/h (3.6%) and 0.93 lb/h (13.6%) was exhibited by nets equipped with Georgia TEDs (with and without funnels, respectively) compared with standard nets. There was no significant difference in shrimp CPUE between standard nets and nets equipped with Super Shooter TEDs with a funnel.

Loss of shrimp by turtle excluder devices (TEDs) in coastal waters of the United States, North Carolina to Texas: March 1988–August 1990

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The National Marine Fisheries Service (NMFS) promulgated regulations which required the use of Turtle Excluder Devices (TEDs) on offshore shrimp vessels beginning in June 1987 (Federal Register 1987), depending upon vessel size, geographic location, and season. In offshore waters, all shrimp trawlers 25 ft and longer must use approved TEDs, and shrimp trawlers smaller than 25 ft are required to restrict tow times to 90 min or less. All shrimp trawlers not pulling TEDs must restrict tow times to 90 min or less in inshore waters. Shrimp trawlers using TEDs are exempt from tow time restrictions in both inshore and offshore waters. TED use in the Gulf of Mexico is required during 1 March–30 November inshore and offshore. In the Atlantic, TEDs are required both inshore and offshore during 1 May–31 August, except for waters off Cape Canaveral and southwest Florida where TEDs are required year-round.

The shrimp fishery in the Gulf of Mexico and southeastern United States is valued at approximately $470 million. Fishing occurs year-round in the Gulf of Mexico, with peak landings in summer for brown shrimp, in fall for white shrimp, and in winter and spring for pink shrimp (Klima et al. 1986, Magnuson et al. 1990). Similarly in the Atlantic, peak landings occur in summer for brown shrimp and in fall for white shrimp (Magnuson et al. 1990).

According to shrimp fishermen, the use of TEDs reduces shrimp catches to the point that their livelihoods are threatened. In 1988, both the Office of Management and Budget (OMB) and the House Appropriations Committee mandated certain studies test-

ing and evaluating the impacts of TED use. The OMB required a study on the efficiency of TEDs in excluding turtles, and the House Appropriations Committee required a study of the full economic impact of TEDs.

NMFS, in cooperation with the shrimp industry, initiated a TED Evaluation Program on 5 March 1988. The objective of this program was to compare shrimp catch rates of TED-equipped trawls with shrimp catch rates of standard trawls in shrimp fishing grounds from North Carolina to Texas. The assumption was that shrimp CPUEs were equal both for vessels from this study and from the commercial fleet fishing during the same seasons and in the same Statistical Areas (Fig. 1). This paper reports on the results of the program and on estimates of total shrimp loss to the fishery through the use of TEDs.

Materials and methods

Recruitment of vessels

Participation in the study by shrimpers was voluntary. Vessels and crews were neither leased nor chartered by NMFS. A payment of $100/d was sometimes provided by the Gulf and South Atlantic Fisheries Development Foundation, generally when TEDs were not required by law. This was an incentive for vessel owners to allow NMFS personnel to collect data while on board their vessels.

Vessels were recruited with the assistance of NMFS port agents, NOAA Sea Grant Marine Advisory agents, regional shrimp associations, and industry contacts. All participating vessels received appropriate federal authorization to use TEDs in only half the trawls when a NMFS observer was on board. Twenty-six quad-rigged vessels (two trawls towed/side) and one twin-rigged vessel (one trawl towed/side) were used in the study.

Areas

Beginning in March 1988, observers were placed on shrimp vessels in each of the four major Gulf of Mexico offshore fishing areas (Louisiana, Texas, south Florida, and Alabama-Mississippi) and in the Atlantic off Florida, Georgia, and North Carolina. Higher levels of observer effort were allocated for areas which historically had higher shrimp production. Of 600 planned observer days, 240 were scheduled for Louisiana, 200 for Texas, 50 each for east and west Florida, and 60 for Mississippi-Alabama. One-hundred observer days were also scheduled for Georgia and North Carolina waters. Observer days were targeted for peak regional shrimping seasons in each area, although this schedule was not always implemented due to constraints of voluntary participation by the shrimp industry.

The U.S. coasts of the Gulf of Mexico and Atlantic Ocean are divided into Statistical Areas (Fig. 1) by NMFS for analytical purposes. Areal groupings for analyses in this study were Statistical Areas 1–8 (West Florida), 9–12 (Florida Panhandle, Alabama, and Mississippi), 13–17 (Louisiana), 18–21 (Texas), 28 (Cape Canaveral), 30–31 (East Florida and Georgia), and 34–35 (North Carolina).

The study depended on shrimpers volunteering to allow NMFS personnel to collect data onboard their vessels. Due to limited response by shrimpers, data came from virtually any vessel whose owner or captain would allow NMFS aboard. Since one of the principal objectives of this study was to evaluate the effect of the use of TEDs on commercial shrimping, the shrimpers decided where and when to fish and which certified TED to use. Our only stipulations were that the shrimper had to use federally approved TEDs, allow gear specialists to properly adjust the TEDs, and keep catches from all nets of

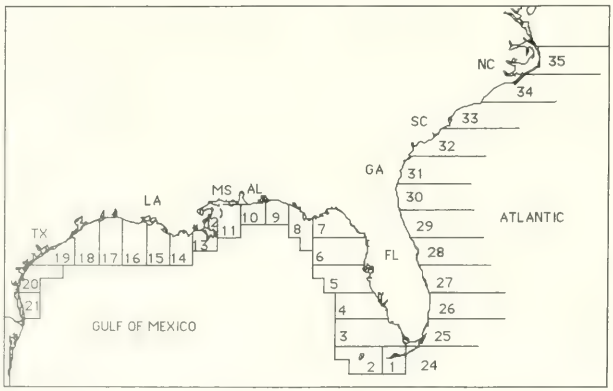

Figure 1
NMFS Statistical Areas in the Gulf of Mexico and Atlantic.

a tow separate to facilitate data collection on deck. The conditions under which the data were collected were assumed to be representative of commercial fishing conditions.

Gear tuning and control tows

The fishing efficiency of all nets used in this study was standardized by NMFS or Sea Grant gear specialists during the initial trip of a participating vessel. Prior to installation of TEDs, control tows were made using standard nets. Lazy line, tickler chain, and float adjustments were made to each net until approximately equal amounts of shrimp were caught by every net.

Vessel captains were instructed by gear specialists on the proper installation of TEDs. Once TEDs were installed, the gear specialist modified the rigging for the proper operation of the TED. This procedure usually required 2–3 d. The captain then was responsible for later gear tuning. Differences in the tuning ability of captains may contribute to variations in the catch data. All Super Shooter TEDs were constructed with accelerator funnels (Fig. 2), i.e., mesh in the shape of a funnel sewn into the net directly in front of the TED. Funnels accelerate water flow through the TED and into the cod end of the net. Georgia TEDs were tested with and without funnels.

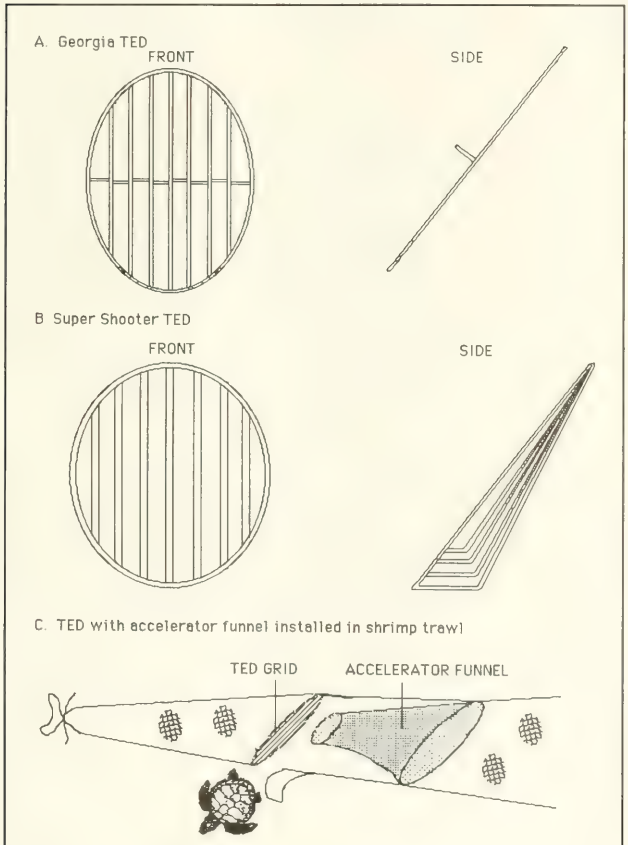

Figure 2
Schematics of Georgia and Super Shooter TEDs and accelerator funnel.

Data collection

Every phase of the operation was explained to vessel captains by NMFS personnel to insure that all data could be collected. Aside from sampling the catch and working up the data, observers did not interfere with normal fishing activity. The primary requirement of the study was that catches from each net be kept separate from all others so the shrimp from each trawl could be weighed and recorded. If necessary, the back deck of the vessel was partitioned with wooden beams to prevent catches from mixing. Captains of the vessels were requested to examine the data collected by the NMFS observer and to sign the data sheets to verify their accuracy.

Shrimp catch on observer vessel A random sample weighing 50–70 lb was shoveled from the contents of each trawl into standard-sized plastic shrimp baskets. Thus, a quad-rigged vessel produced four samples per tow and a twin-rigged vessel two samples per tow. Shrimp were separated from each sample and total weight (to the nearest lb) of brown, pink, and white shrimp (*Penaeus* sp.) combined was recorded for every net of each tow. No analysis by species was possible or proposed by this study. If the shrimper discarded small shrimp, observers were instructed to include only the size-range of shrimp retained by the shrimpers for their weights. Catch was recorded as heads-on or heads-off. Heads-off weight = (0.63 heads-on weight).

For each tow, shrimp CPUE (heads-off lb/h/100 ft of headrope towed) from all TED-equipped nets were averaged and compared against the average shrimp CPUE of all standard nets, to provide one TED-standard data pair per tow. Unless otherwise stated, shrimp CPUE will refer to heads-off lb/h/100 ft of headrope. The average CPUEs of two TED-equipped and two standard nets were paired for each tow for 26 quad-rigged vessels and 1 twin-rigged vessel. However, if one net was excluded from the analysis due to unacceptable operation (refer to Gear Performance), then the CPUE value from the remaining net was paired with the average of CPUEs from the other two nets. If both nets of a given gear type malfunctioned, all data from that tow were deleted from the analysis. Standard and experimental nets were compared on twin-rigged vessels and these data pooled with those from quad-rigged vessels.

Commercial shrimp catch Effort data for a given temporal and spatial area were calculated by taking the average trip CPUEs (heads-off lbs/24 h day/4 nets), obtained by interviewing vessel captains, and extrapolating to total effort by using the total-pounds value from dealers' records. Fishing-effort data on the shrimp fleet have been collected in this manner since 1960. These data were compared with CPUEs (heads-off lbs/24 h day/4 nets) from our observer trips. The assumption that shrimp CPUEs were equal, both for vessels from this study and from the commercial fleet fishing during the same seasons and in the same Statistical Areas, was tested using a paired t-test with a probability level of 0.05.

Gear performance Each net was characterized by an operation code based on its performance in the water. Codes were used to describe successful tows or problems encountered, such as tangling of trawl doors, gear fouling, twisted cables, bag choking, etc. Two codes were occasionally required to describe trawl performance.

Data collected from the problematic tows not related to TEDs, e.g., cod end coming untied, gear not fishing properly, torn nets, and broken cables, were not included in the analyses. Chi-square ($P<0.05$) analysis was used to determine if the problematic tows were independent of net type (e.g., TED-equipped nets or standard nets) by area (Gulf of Mexico or Atlantic).

Statistical analyses

Paired t-tests Paired t-tests were performed to test the hypothesis of equal CPUE of shrimp by standard and TED-equipped trawls. Data were paired by tow. Confidence intervals (95%) on CPUE were also calculated.

Biological models Deterministic population models were produced for brown shrimp *Penaeus aztecus*, white shrimp *P. setiferus*, and pink shrimp *P. duorarum* by linking a Ricker-type yield-per-recruit model to recruitment estimates that were independent of parent stock (Ricker 1975, Nichols 1984, Nance & Nichols 1988). Recruitment level was set at the geometric mean for the complete data set (1960–88). Estimates for 1986–89 fishing mortality rates (F) were derived from virtual population analysis, and the average was used as the baseline for current conditions. Yield estimates were made for all three species for a range of "F-multiplier" values of 0–2 by 0.02 increments. Tables of these yield estimates were used to determine effects of TED-equipped nets on the shrimp yield in the Gulf of Mexico. This was possible because yield estimates (Y_t) are a direct result of fishing mortality rates (Royce 1972). The yield model was

$$Y_t = F_t N_t W_t dt ,$$

where N_t is the number of animals (R) in a cohort subject to fishing (F) and natural (M) mortality at a given time (t), using the formula

$$N_t = Re^{-(F+M)(t-t_0)},$$

F_t = fishing mortality at a given time,

W_t = average weight of an individual at time t, estimated from growth equations.

Fishing mortality rate (F) is the product of two separate variables, a catchability coefficient (q) and directed nominal fishing effort (f):

$$F = qf.$$

TED-equipped nets influence fishing mortality (F) by affecting shrimp catchability (q), and not fishing effort (f). Any percentage change in shrimp catchability caused by TED-equipped nets was assumed to be directly reflected in an equal percentage change in fishing mortality. This is based on an assumption of direct proportionality between change in CPUE and change in q. Thus, any change in CPUE as a result of TED use is translated into a proportional change in q.

Results

Descriptive data summary

Paired data In the Gulf of Mexico, 589 data pairs were collected using Georgia TEDs equipped with accelerator funnels, 59 pairs from Georgia TEDs without funnels, and 50 pairs from Super Shooter TEDs with

Table 1

Frequency of paired tows for standard nets and nets equipped with Super Shooter TEDs with funnel (SF), Georgia TEDs with funnel (GF), and Georgia TEDs without funnels (G) by season and area.

	Winter			Spring			Summer			Fall		
Areas*	SF	GF	G	SF	GF	G	SF	GF	G	SF	GF	G
WFL (1–8)	2	17	–	15	79	10	–	–	–	–	–	–
MAFP (9–12)	–	28	–	11	3	–	–	20	–		39	–
LA (13–17)	–	60	–	22	55	–	–	25	21	–	104	–
TX (18–21)	–	3	5	–	1	–	–	88	–		67	23
CCFL (28)	–	–	60	–	–	–	–	–	–	–	–	–
EFLG (30–31)	–	30	–	–	–	–	–	21	163	–	35	–
NC (34–35)	–	–	–	–	–	–	186	–	–	–	–	–
Totals	2	138	65	48	138	10	186	154	184	0	245	23

* Areas 1–8 (West Florida), 9–12 (Florida Panhandle, Alabama, Mississippi), 13–17 (Louisiana), 18–21 (Texas), 28 (Cape Canaveral), 30–31 (East Florida and Georgia), and 34–35 (North Carolina).

funnels. There were 86 and 223 data pairs in the Atlantic for Georgia TEDs with and without accelerator funnels, respectively, and 186 pairs for Super Shooter TEDs with funnels. Frequencies of data collection by geographic area and season (winter: December–February, spring: March–May, summer: June–August, fall: September–November) are presented in Table 1.

Performance of TED-equipped and standard nets Data were collected from 5937 nets during the 2.5 yr study. Frequency of net problems was tabulated by TED type. The most frequent problems included clogging of the net, twisting of trawl doors and cables, and torn webbing. In the Gulf of Mexico, no problems occurred during 86%, 87%, 75%, and 87% of the tows for nets equipped with Georgia TEDs with and without funnels, Super Shooter TEDs and standard nets, respectively (Table 2). In the Atlantic, the values were 96%, 90%, 89%, and 95% for the respective gear types (Table 2). A variety of problems, including but not limited to those with trawl doors, cables, bogging-down of nets, etc., were shown to be net-type independent (e.g., TED-equipped nets or standard nets) in the Gulf of Mexico and net-type dependent in the Atlantic (chi-square, $P<0.05$).

Table 2

Comparison of net types and gear-related problems in the Gulf of Mexico and Atlantic for Georgia TEDs with (GF) and without (G) funnels, Super Shooter TED with funnel (SF), and standard shrimp nets (STD). Sample includes all nets used from all vessels during the study. Values represent the percent of nets in each category; totals may not equal 100% due to rounding.

	STD	G	GF	SF
	(n=2356)	(n=199)	(n=1243)	(n=185)
Gulf of Mexico				
None	87	87	86	75
Clogging, choking	4	4	6	7
Doors, cables	4	5	5	2
Torn webbing	3	4	2	4
Other	2	0	1	12
Atlantic				
None	95	90	96	89
Clogging, choking	3	0	3	6
Doors, cables	2	10	0	4
Torn webbing	1	0	0	1

Testing of paired tows

Reduction of shrimp CPUE associated with use of TEDs Mixtures of brown and white shrimp were captured in all areas of the Gulf and Atlantic, except for the west coast of Florida where pink shrimp were prevalent. Shrimp species were not separated for analyses.

There was no significant difference ($P<0.05$) in net sizes among vessels in this study, so this parameter was excluded from any further analyses. Summaries of shrimp CPUEs by TED type, season, and area are presented in Tables 3–5. Mean shrimp CPUEs for Geor-

Table 3

Comparisons (paired *t*-test) between shrimp CPUE (heads-off lbs/h/100 ft headrope) of standard (STD) and Super Shooter-equipped nets with accelerator funnel. *N* = number of tows.

		Mean CPUE			Gain (loss) by use of TED	
	N	STD net	TED net	*P*	CPUE	Percent
Overall	236	11.41	11.25	0.58	(–0.16)	(–1)
Seasons*						
Winter	2	16.74	15.79	—	(–0.95)	(–6)
Spring	48	8.70	8.57	0.69	(–0.12)	(–1)
Summer	186	12.05	11.89	0.66	(–0.16)	(–1)
Areas**						
1–8	17	13.92	12.70	0.01	(–1.22)	(–9)
9–12	11	2.44	2.63	0.06	0.19	+8
13–17	22	8.52	9.00	0.12	0.48	+6
33–35	86	12.05	11.89	0.70	(–0.16)	(–1)

* Winter (December–February), Spring (March–May), Summer (June–August), Fall (September–November).

** Areas 1–8 (West Florida), 9–12 (Florida Panhandle, Alabama, Mississippi), 13–17 (Louisiana), 18–21 (Texas), 28 (Cape Canaveral), 30–31 (East Florida and Georgia), and 34–35 (North Carolina).

Table 4

Comparisons (paired *t*-test) between shrimp CPUE (heads-off lbs/h/100 ft headrope) of standard (STD) and Georgia TED-equipped nets **with** accelerator funnel. *N* = number of tows.

		Mean CPUE			Gain (loss) by use of TED	
	N	STD net	TED net	*P*	CPUE	Percent
Overall	674	6.66	6.42	0.02	(–0.24)	(–4)
Seasons*						
Winter	138	4.12	4.46	<0.01	0.34	+8
Spring	138	4.51	3.95	<0.01	(–0.56)	(–12)
Summer	154	9.23	8.56	<0.01	(–0.67)	(–7)
Fall	244	7.70	7.58	0.82	(–0.12)	(–2)
Areas**						
1–8	96	5.22	4.69	0.01	(–0.53)	(–10)
9–12	90	7.53	7.18	0.21	(–0.35)	(–5)
13–17	244	5.69	5.40	<0.01	(–0.29)	(–5)
18–21	158	7.42	7.40	0.99	(–0.02)	(–0)
28	86	8.77	8.67	0.84	(–0.10)	(–1)

* Winter (December–February), Spring (March–May), Summer (June–August), Fall (September–November).

** Areas 1–8 (West Florida), 9–12 (Florida Panhandle, Alabama, Mississippi), 13–17 (Louisiana), 18–21 (Texas), 28 (Cape Canaveral), 30–31 (East Florida and Georgia), and 34–35 (North Carolina).

Table 5

Comparisons (paired *t*-test) between shrimp CPUE (heads-off lbs/h/100 ft headrope) of standard (STD) and Georgia TED-equipped nets **without** accelerator funnel. *N* = number of tows.

		Mean CPUE			Gain (loss) by use of TED	
	N	STD net	TED net	*P*	CPUE	Percent
Overall	284	6.77	5.84	<0.01	(–0.93)	(–14)
Seasons*						
Winter	65	4.77	4.59	0.52	(–0.18)	(–4)
Spring	10	6.06	3.86	0.25	(–2.20)	(–36)
Summer	186	7.66	6.53	<0.01	(–1.13)	(–15)
Fall	23	5.48	4.78	<0.01	(–0.70)	(–13)
Areas**						
1–8	10	6.06	3.86	0.25	(–2.20)	(–36)
13–17	21	8.71	8.74	0.99	+0.03	+0
18–21	28	5.76	5.10	<0.01	(–0.66)	(–11)
28	76	8.06	7.20	0.10	(–0.86)	(–11)
29–32	147	6.06	5.04	<0.01	(–1.02)	(–17)

* Winter (December–February), Spring (March–May), Summer (June–August), Fall (September–November).

** Areas 1–8 (West Florida), 9–12 (Florida Panhandle, Alabama, Mississippi), 13–17 (Louisiana), 18–21 (Texas), 28 (Cape Canaveral), 30–31 (East Florida and Georgia), and 34–35 (North Carolina).

gia TED-equipped nets were 6.42 lb/h (TED with funnel) and 5.84 lb/h (TED without funnel). Paired standard nets caught 6.66 lb/h and 6.77 lb/h, respectively, exhibiting statistically-significant gains of 0.24 and 0.93 lb/h. Comparison of standard and Super Shooter TED-equipped nets showed a mean shrimp CPUE of 11.41 lb/h and 11.25 lb/h, respectively, for a statistically-non-significant loss of 0.16 lb/h with the Super Shooter TED.

Seasons CPUEs varied among seasons, just as abundance of shrimp on the fishery grounds varied among seasons. Shrimp CPUEs from standard nets and nets equipped with Super Shooter TEDs were not significantly different (Table 3). However, differences in shrimp CPUE between standard nets and nets with Georgia TEDs were significant during winter, spring, and summer. These values ranged from a gain of 0.34 lb/h to a loss of 0.67 lb/h by Georgia TED-equipped nets with a funnel (Table 4) and a loss of 0.70–1.13 lb/h by Georgia TED-equipped nets without a funnel (Table 5). CPUE differences due to TEDs were so small that they were likely masked by natural variations in shrimp CPUE.

Areas In most areas of the study, shrimp catch rates for TED-equipped nets were comparable with those for standard nets (Tables 3–5). Statistically-significant reductions (1.2 and 0.5 lb/h) in shrimp CPUE occurred off west Florida in nets equipped with Super Shooter TEDs and Georgia TEDs with funnels, respectively. Off Louisiana, standard nets caught 0.3 lb/h more shrimp than the paired Georgia TED-equipped nets with funnels. Shrimp CPUE was higher by 0.7 and 1.0 lb/h for standard nets paired with Georgia TED-equipped nets without funnels offshore of Texas and the east coast (Florida and Georgia), respectively.

CPUE comparisons with commercial shrimp fleet in the Gulf of Mexico Average shrimp CPUE (heads-off lbs/24 h day/4 nets) by Statistical Area groupings and seasonal groupings for standard nets was compared with CPUE (heads-off lbs/24 h day/4 nets) for standard nets on other commercial vessels fishing in the same area and season in the Gulf of Mexico. Our initial assumption that our data were representative of commercial fishing conditions was supported by standard net CPUEs on commercial observer vessels that were not significantly different (paired t-test, $P>0.05$) from CPUEs on commercial vessels without observers. Mean differences ranged from a 6.2 lb/h gain by standard nets on TED observer vessels to a 4.9 lb/h gain by standard nets on other commercial vessels. In three of seven season/area combinations, shrimp CPUE from TED-observer vessels was higher than CPUEs of other commercial vessels. Since there were no significant differences in net size during our study, we assumed that this was the case for the rest of the commercial fleet. TED-observer vessels were apparently representative of other commercial vessels in the fleet fishing in similar areas during the same season. Similar analyses for the Atlantic fishery could not be made since catch information was not available on a trip-by-trip basis.

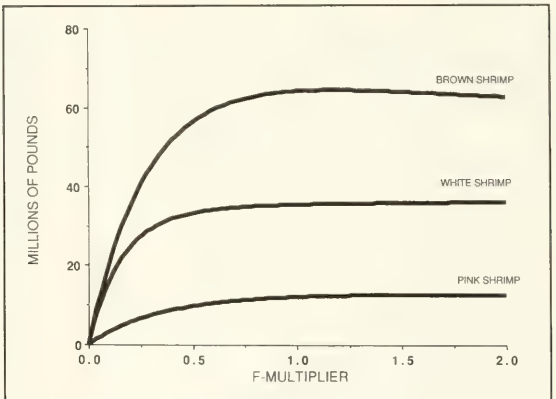

Figure 3
Yield models for brown *Penaeus aztecus*, white *P. setiferus*, and pink *P. duorarum* shrimp.

Biological yield models

Ricker-type yield models (Ricker 1975) developed for each of the three major shrimp species show the same basic curve shape (Fig. 3; Nance & Nichols 1988). The curves are asymptotic where yield estimates are plotted for current fishing mortality rates (F-multiplier = 1.0). Thus, with current fishing patterns and current fishing mortality rates, little increase or decrease in yield is predicted with the minor reductions in F that would be expected due to small losses of shrimp by TEDs.

Yield estimates were calculated in the model by varying the F-multiplier in increments of 0.02. Mean shrimp loss with TED-equipped vs. standard nets varied from 1 to 14% by TED type. A decrease of 5% in F would result in an undetectable change in annual yield in the brown or white shrimp fisheries and a 1% reduction in the annual yield of the pink shrimp fishery in the U.S. Gulf of Mexico.

Discussion

Our data were collected by NMFS observers during cooperative cruises with shrimp industry participants. Since this was a voluntary program, TED type, area, and season of sampling were controlled by industry participants. Data came from virtually any vessel whose owner or captain would allow NMFS observers aboard.

Not all federally approved TED types were tested. If a shrimper could not maintain TED efficiency during a trip, the trip was aborted by the shrimper or the TED was not used again. This resulted in nominal imbalances in the data by area, season, and TED type, including some data sets too small for analysis.

Mean shrimp catch rates in TED-equipped nets were lower than those in standard nets, varying from a loss of 1.4% with Super Shooter TEDs to a loss of 13.6% for Georgia TEDs without funnels. Nets equipped with Georgia TEDs without a funnel were used mainly dur-

ing the first 6 months of this study. Higher losses of shrimp from these nets may be due to (1) initial inexperience by shrimpers using TEDs, (2) high losses of shrimp in rough-bottom areas, and (3) absence of a funnel in the TED. The lack of an accelerator funnel to assist shrimp movement past the escape opening of the TED could also account for some shrimp loss. The Georgia TED with an accelerator funnel exhibited a 3.6% reduction in shrimp CPUE compared with 13.6% by the Georgia TED without a funnel. Nets equipped with the Super Shooter TED exhibited the lowest reduction (1.4%) in shrimp CPUE when compared with the standard nets. This may have been due to (1) shrimpers having more experience with TEDs when this model was introduced during the second year of the study, and (2) more effective shrimp retention by the TED. The Super Shooter design also reduces clogging of TED bars by seagrasses and algae and may reduce shrimp loss. Although this TED exhibited the lowest reduction in shrimp CPUEs, it accounted for more problems during trawling than the other TEDs. These problems evidently did not affect shrimp catchability, since there was no significant difference between its catch rate and that of the paired standard net.

Areal differences in shrimp abundance may be confounded with CPUEs due to different types of TEDS and standard nets (flat nets, semiballoon nets, mongoose nets, etc.). Some TEDs work better on hard-bottom than on soft-bottom or with different types and abundances of bycatch. Georgia TEDs with funnels were the most common TED tested in Texas, Louisiana, and Florida. Super Shooter TEDs with funnels were used in North Carolina. The effectiveness of the TED type does influence the catch rates of shrimp.

Phares (1978), in describing the selectivity of shrimp nets, indicated that loss rates varied by area and season and affected an extensive size-range of lost shrimp. We have assumed (1) that shrimp escaping through either a TED-equipped net or a standard net will not die because of that episode, and (2) that escaping shrimp will grow and experience the same subsequent natural and fishing mortality as the rest of the stock. Thus, survival rates of shrimp escaping through the cod end of a standard net should be the same as those of shrimp escaping through the cod end of a TED net. Shrimp escaping through TED openings probably are not injured and are subject to subsequent recapture. Although decreases in CPUE may impact a given fisherman on any particular tow, these lost shrimp will still be available to fishermen for capture by succeeding tows.

Mathematical models indicated that a TED-induced decrease of 5% in F would result in an undetectable change in yield in the brown or white shrimp fisheries and a 1% reduction in the annual yield of the pink shrimp fishery in the U.S. Gulf of Mexico. Because of the asymptotic nature of the yield curves, only slight decreases in yield would be observed in some shrimp fisheries even if loss rates from TEDs were in the 10–20% range. With a 10% loss rate, we calculated a reduction from the pink shrimp fishery of 2% and no decreases in yield from either the white or brown shrimp fisheries. A 20% loss rate would result in a 4% reduction of the annual yield of pink shrimp and a 1–2% reduction for brown and white shrimp fisheries.

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Abstract.—Food habits data from 415 sandbar sharks collected in the area between Cape Hatteras and Georges Bank (Great South Channel) were examined. Mean fork length (FL) and body weight (BW) were 55.0 cm and 1.72 kg for pups, 123.0 cm and 23.0 kg for juveniles, and 166.0 cm and 52.3 kg for adults. Of all juvenile and adult stomachs, 49% contained prey, primarily fish (teleosts and skates). Of stomachs from pups, 80% held food remains consisting almost exclusively of soft blue crabs. The mean percentage of stomach content volume to BW is 1.16 for pups, and 0.42 for juveniles and adults. Daily ration estimates as percentage of mean BW are 1.43 for pups, and 0.86 for juveniles and adults. Annual food consumption is estimated to be 5.1 times the mean BW for pups, and 3.1 times for juveniles and adults.

Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration*

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The sandbar shark *Carcharhinus plumbeus* is a medium-sized species found in temperate and subtropical waters of the world's oceans and the Mediterranean Sea. It occurs from nearshore out to a depth of at least 250 m (Springer 1960, Garrick 1982). Evidence of its occurrence over deep water is provided by Springer (1960) who reports the capture of three specimens taken in midwater over depths of 1000–1800 m. Distribution of the sandbar shark along the U.S. east coast extends from Massachusetts to the Florida Keys in the summer and from the offings of the Carolinas to Cape Canaveral during the winter months (Bigelow & Schroeder 1948, Springer 1960). From May through September, newborn pups and small juveniles (<100 cm fork length, FL) are common to abundant in shallow bays and estuarine systems along the coast from Long Island, New York to Cape Canaveral, Florida. With the approach of autumn, young sharks migrate offshore and south to winter at depths approaching 137 m (Springer 1960, Medved & Marshall 1983). Casey (1976) and Casey et al. (1985) showed that when the juvenile sandbar sharks attain a size of about 110 cmFL, they no longer frequent the shallow nursery areas but remain off the coast, demonstrating more extensive seasonal migrations with increasing size.

The most detailed publications to date on food and feeding in the sandbar shark come from Springer (1960), Medved & Marshall (1983), Medved (1985), and Medved et al. (1985, 1988). These papers are important contributions to our knowledge of the diet, feeding behavior, and daily ration of young sandbar sharks and what impact they have on prey resources in the estuaries and nearshore areas. The first study to estimate digestion rate in the sandbar shark was conducted by Wass (1973) in a seawater enclosure at the Kewalo Basin facility in Hawaii.

The purpose of this paper is to present data on the food and feeding habits of sandbar sharks occurring from Georges Bank (Great South Channel) to Cape Hatteras, to define dietary differences and energy needs of pups, juveniles, and adults, and to estimate their daily ration.

Methods

Stomachs were sampled from 1972 through 1984 during (1) shark fishing tournaments held at several coastal ports from Rhode Island to southern New Jersey, (2) on cruises using

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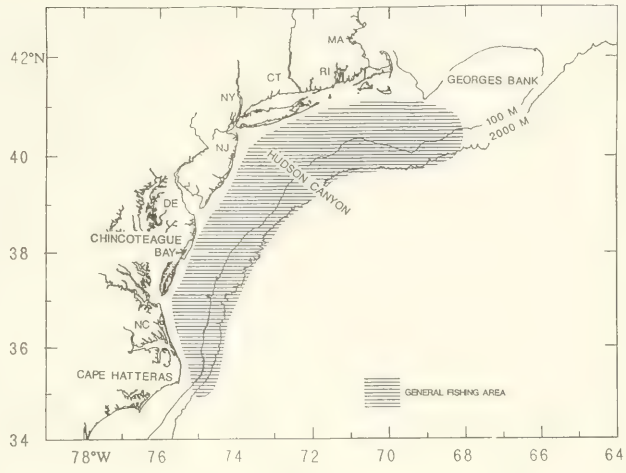

Figure 1

Fishing area off the U.S. northeast coast where 415 sandbar shark *Carcharhinus plumbeus* pups, juveniles, and adults were caught and examined for food habits studies, 1972–84. The 100 m depth contour separates the nearshore and offshore sampling areas.

longline gear aboard research and commercial fishing vessels from Cape Hatteras to Georges Bank, and (3) during a 6 d period of fishing at the end of June 1983 with rod-and-reel in Chincoteague Bay, Virginia (Fig. 1). Collections and examinations of all stomachs were made during March to September, with the majority being taken in June and July. Stomachs were excised and the volume of the contents (liquid and solids) measured as soon after capture as possible. Solid remains were drained, sorted, and identified to the lowest taxon possible, then enumerated and measured volumetrically by water displacement in a graduated beaker. A conversion of 1 mL=1 g was used to convert volume to weight for comparisons with shark body weights. Major forage categories were expressed as percentages by number of particular prey items, as total volume of the prey items, and as frequency of their occurrence (number of stomachs). Maximum capacity was estimated by filling the stomachs with water under low pressure, then measuring the volume of water in a graduated container. The maximum capacities of stomachs from Chincoteague Bay sharks were not determined because a pressurized water system was not available. Analysis of the data for differences in prey, food volumes by area, and daily ration was accomplished by separating the samples into three groups: Chincoteague Bay, nearshore (<100 m), and offshore (>100 m) (Fig. 1). The Chincoteague sample was further separated into two distinct age classes: newborn pups (estimated <3 d-old) and small juveniles (>3 d–3+ yr). Newborn pups were distinguished by pale, unpigmented edges on the fins, unhealed or partially-healed umbilical openings, and the presence of large cream-colored livers that floated slightly above the surface when placed in seawater. "Older" pups and small juveniles had livers that were reduced in size, varied in color from tan to gray-green, and sank slowly or floated just beneath the water surface. In addition, their umbilical openings were completely healed, visible only as white streaks 5–6 mm long. Juveniles and adults of both sexes were separated, based on a minimum reproductive size of 150 cmFL (Casey et al. 1985).

Results and discussion

Stomachs from 415 sandbar sharks were examined, including 321 from nearshore (268) and offshore (53) waters between Cape Hatteras, North Carolina and Georges Bank, and 94 from Chincoteague Bay, Virginia.

Analysis of nearshore and offshore samples

In the nearshore area, juvenile males and females and adult females were represented by almost equal numbers, i.e., 81, 84, and 89, respectively, whereas only 12 adult males were sampled. Offshore, juvenile males were most abundant (37), with adult males represented by four individuals. Females were limited to four adults and eight juveniles. Mean fork length (FL) and body weight (BW) of sandbar sharks for the whole sample were 138 cm (range 69.0–212.0) and 34.0 kg (3.0–145.0) (Table 1). Offshore, only juvenile males were numerous enough in the sample to derive reliable mean values.

Prey analysis Prey consumed by sandbar sharks in the study area consists primarily of benthic and demersal species, both vertebrate and invertebrate (Table 2). Of the 40 different prey types observed in

Table 1

Average fork lengths and body weights for 321 juvenile and adult sandbar sharks *Carcharhinus plumbeus* examined from nearshore (<100 m) and offshore (>100 m) waters of the U.S. northeast coast between Cape Hatteras and Georges Bank, 1972–84.

		Overall mean	Overall mean by sex		Adults			Juveniles		
		Overall mean	Male	Female	All	Male	Female	All	Male	Female
Total sample	[a]*N*	321	134	185	110	16	94	211	118	91
	[b]FL	138.0	125.0	147.5	166.0	156.3	167.6	123.0	120.8	126.0
	N	288	107	180	108	15	93	180	92	87
	[c]BW	34.0	23.8	40.3	52.0	40.0	54.3	23.0	21.0	25.0
Nearshore	*N*	268	93	173	102	12	90	166	81	83
	FL	142.3	130.5	149.0	165.0	157.0	166.0	128.3	126.5	130.4
	N	252	83	168	101	12	89	151	71	79
	BW	35.6	26.5	40.2	50.0	40.0	52.0	25.7	24.2	27.2
Offshore	*N*	53	41	12	8	4	4	45	37	8
	FL	114.5	112.6	120.5	178.3	153.5	203.2	103.0	108.0	79.0
	N	36	20	12	7	3	4	29	21	8
	BW	22.8	14.0	40.3	79.8	39.0	110.5	9.0	10.6	5.2

[a]*N* = number of sharks.
[b]FL = mean fork length in cm.
[c]BW = mean body weight in kg.

the stomachs, only six occurred in both the near- and offshore areas (Tables 3, 4), including squids, skates, skate egg cases, goosefish *Lophius americanus*, bluefish *Pomatomus saltatrix*, and Bothidae (flatfish). Summarizing the prey into major food groups (Fig. 2) shows that 43.0% (by frequency of occurrence) of the food was composed of teleosts, followed by elasmobranchs (16%), cephalopods (3.0%), and miscellaneous organisms and trash (pebbles, seagrass, paper scraps; 5.0%). The size of prey ingested appears to be an important factor in its selection, since the majority of prey items observed in the stomachs were small enough to be swallowed whole. Those that were consumed as bite-sized portions included larger skates, goosefish, bluefish, and smooth dogfish *Mustelus canis* and spiny dogfish *Squalus acanthias*. These food items were eaten by the larger juveniles and adults only. Earlier reports by Bigelow & Schroeder (1948), Springer (1960), Bass et al. (1973), and Lawler (1976) also indicate that small fish and invertebrates are most common in the diet. Springer (1960) adds that fresh fish is preferred over stale or decomposed fish and mammal flesh.

Teleosts The food group 'All Teleosts' (Fig. 2) was composed of species ranging from sedentary (goosefish) to actively-swimming forms (bluefish, mackerel *Scomber scombrus*). Flatfish (flounders) from the families Bothidae and Pleuronectidae occurred with the highest (10.0%) frequency overall (Fig. 2). Predation on these two families was most evident in sharks collected nearshore (Table 3). Goosefish comprised the second most-important fish in the diet by frequency of occurrence (6.0%) and was consumed by juvenile and adult sharks (Fig. 2). Goosefish remains varied from small (4 cmTL) to medium-sized (45 cmTL) individuals that were eaten in chunks. Remains of this prey item occurred most often in sandbar shark stomachs collected off the Long Island (NY) and New Jersey coasts. Bluefish occurred in nine stomachs (3.0%), seven of which were from females captured nearshore. Gadids consisted principally of hakes digested beyond species recognition, except for one silver hake *Merluccius bilinearis* that was relatively fresh. Scombrids occurred in seven stomachs (Fig. 2) and consisted almost exclusively of identifiable remains of common mackerel. The occurrence of fast-swimming scombrid species in stomachs agrees with the reported occurrence of bonito *Sarda sarda* [and weakfish *Cynoscion regalis*] by Bigelow & Schroeder (1948). "Other Teleosts" (Fig. 2), comprising 20.0% of the food by frequency of occurrence, is a group composed of at least 12 species from Table 1, each occurring infrequently in the diet but representative of local availability. Of this food category, 14% (by frequency of occurrence) also included fish remnants that could not be identified to family or species.

Table 2

Stomach contents from 321 sandbar sharks *Carcharhinus plumbeus* captured in nearshore (<100 m) and offshore (>100 m) waters between Cape Hatteras and Georges Bank.

	Food		Items		Stomachs	
	Vol. (mL)	%	*N*	%	*N*	%
Arthropoda						
Cancridae						
Cancer sp.	93	0.20	3	1.03	3	0.93
Unident. crab	1	0.00	1	0.34	1	0.31
Isopoda	8	0.02	10	3.46	1	0.31
Cephalopoda						
Gonatidae	120	0.26	1	0.34	1	0.31
Ommastrephidae	6	0.01	1	0.34	1	0.31
Illex illecebrosus	70	0.15	2	0.69	2	0.62
Unident. squids	141	0.30	9	3.11	7	2.18
Echinoderma						
Scutellidae (sand dollars)	13	0.02	4	1.38	3	0.93
Elasmobranchs						
Squalus acanthias	246	0.53	6	2.07	4	1.24
Mustelus canis	2365	5.12	1	0.34	1	0.31
Raja erinacea	6785	14.71	17	5.88	13	4.05
Raja sp.	5190	11.25	26	9.00	25	7.78
Dasyatidae	175	0.37	1	0.34	1	0.31
Skate eggs	192	0.41	11	3.80	7	2.18
Teleosts						
Congridae	925	2.00	1	0.34	1	0.31
Ophichthus cruentifer	55	0.11	13	4.49	2	0.62
Clupeidae	80	0.17	1	0.34	1	0.31
Chauliodontidae	75	0.16	1	0.34	1	0.31
Lophius americanus	7445	16.14	23	7.95	20	6.23
Synodontidae	75	0.16	3	1.03	3	0.93
Gadidae	1975	4.28	9	3.11	6	1.86
Merluccius bilinearis	100	0.21	1	0.34	1	0.31
Carangidae	50	0.10	1	0.34	1	0.31
Cottidae	965	2.09	6	2.07	3	0.93
Labridae	25	0.05	1	0.34	1	0.31
Ophidiidae	30	0.06	1	0.34	1	0.31
Pomatomus saltatrix	2792	6.05	9	3.11	9	2.88
Scombridae	50	0.97	1	0.34	1	0.31
Scomber scombrus	1410	3.05	6	2.07	6	1.86
Peprilus triacanthus	100	0.21	2	0.69	1	0.31
Triglidae	14	0.03	1	0.34	1	0.31
Zoarcidae	410	0.88	1	0.34	1	0.31
Macrozoarces americanus	350	0.75	1	0.34	1	0.31
Bothidae	1330	2.88	5	1.73	5	1.55
Limanda ferruginea	4627	10.03	21	7.26	8	2.49
Pleuronectidae	2780	6.02	20	6.92	18	5.60
Teleost unident.	4163	9.02	60	20.76	47	14.60
Miscellaneous						
Clam Shells	55	0.12	2	0.69	2	0.62
Marine mammal flesh	50	0.10	1	0.34	1	0.31
Animal remains	390	0.80	4	1.38	4	1.24
Trash	1	0.00	1	0.34	1	0.31
Totals	46,127		289			

Table 3

Stomach contents from 268 sandbar sharks *Carcharhinus plumbeus* captured in nearshore (<100 m) waters between Cape Hatteras and Georges Bank.

	Food		Items		Stomachs	
	Vol. (mL)	%	*N*	%	*N*	%
Arthropoda						
Cancridae						
Cancer sp.	93	0.22	3	1.37	3	1.10
Unident. crab	1	0.00	1	0.45	1	0.37
Cephalopoda						
Gonatidae	120	0.28	1	0.45	1	0.37
*Unident. squid	40	0.09	5	2.28	3	1.11
Echinoderma						
Scutellidae (sand dollars)	13	0.03	4	1.82	3	1.11
Elasmobranchs						
Squalus acanthias	180	0.42	2	0.91	2	0.75
Mustelus canis	2365	5.64	1	0.45	1	0.37
Raja erinacea	6785	16.20	17	7.76	13	4.80
**Raja* sp.	5140	12.27	25	11.41	24	8.95
*Skate eggs	186	0.44	9	4.10	6	2.20
Teleosts						
Congridae	925	2.20	1	0.45	1	0.37
Clupeidae	80	0.19	1	0.45	1	0.37
Chauliodontidae	75	0.17	1	0.45	1	0.37
**Lophius americanus*	5870	14.02	20	9.13	17	6.30
Synodontidae	75	0.17	3	1.36	3	1.10
Gadidae	1450	3.46	4	1.82	4	1.50
Merluccius bilinearis	100	0.23	1	0.45	1	0.37
Carangidae	50	0.11	1	0.45	1	0.37
Cottidae	965	2.30	6	2.73	3	1.10
Labridae	25	0.05	1	0.45	1	0.37
Ophidiidae	30	0.07	1	0.45	1	0.37
**Pomatomus saltatrix*	2765	6.60	8	3.65	8	3.00
Scomber scombrus	1410	3.36	6	2.73	6	2.20
Peprilus triacanthis	100	0.23	2	0.91	1	0.37
Zoarcidae	410	0.97	1	0.45	1	0.37
Macrozoarces americanus	350	0.83	1	0.45	1	0.37
*Bothidae	730	1.73	4	1.82	4	1.50
Limanda ferruginea	4627	11.05	21	9.58	8	3.00
Pleuronectidae	2780	6.64	20	9.13	18	6.71
Teleost unident.	3676	8.78	41	18.72	37	13.80
Miscellaneous						
Clam shells	55	0.13	2	0.91	2	0.75
Marine mammal flesh	50	0.11	1	0.45	1	0.37
Animal remains	340	0.81	3	1.36	3	1.10
Trash	1	0.00	1	0.45	1	0.37
Totals	41,862		219			

Note: Asterisk indicates prey items duplicated offshore.

Table 4

Stomach contents from 53 sandbar sharks *Carcharhinus plumbeus* captured offshore (>100m) between Cape Hatteras, North Carolina, and Georges Bank.

	Food		Items		Stomachs	
	Vol. (mL)	%	*N*	%	*N*	%
Arthropoda						
Isopoda	8	0.18	10	14.28	1	1.90
Cephalopoda						
Ommastrephidae	6	0.14	1	1.42	1	1.90
Illex illecebrosus	70	1.64	2	2.85	2	3.77
*Unident. squid	101	2.36	4	5.71	4	7.54
Elasmobranchs						
Squalus acanthias	66	1.54	4	5.71	2	3.77
**Raja* sp.	50	1.17	1	1.42	1	1.90
Dasyatidae	175	4.10	1	1.42	1	1.90
*Skate eggs	6	0.14	2	2.85	1	1.90
Teleosts						
Ophichthus cruentifer	55	1.28	13	18.57	2	3.77
Gadidae	525	12.50	5	7.14	2	3.77
**Lophius americanus*	1575	36.92	3	4.28	3	5.66
**Pomatomus saltatrix*	27	0.63	1	1.42	1	1.90
Scombridae	450	10.55	1	1.42	1	1.90
Triglidae	14	0.32	1	1.42	1	1.90
*Bothidae	600	14.06	1	1.42	1	1.90
Teleost unident.	487	11.41	19	27.14	10	18.86
Miscellaneous						
Animal remains	50	1.17	1	1.42	1	1.90
Totals	4265		70			

Note: Asterisk indicates prey items duplicated nearshore.

Elasmobranchs Elasmobranchs ranked second to teleosts as a major food group, accounting for 16.0% of the food by frequency of occurrence (Fig. 2). Skates of the family Rajidae were the principal representatives in this food group, with *Raja erinacea* occurring most frequently. Unspecified skate remains described as *Raja* spp. in Table 2 most likely included *R. erinacea* and possibly *R. eglanteria*, both which commonly occur in the sampling area. Eleven skate egg cases were also found in seven stomachs. These were generally torn and old looking. However, a few contained yolk material suggesting they were ingested as a food source rather than by accident. Based on frequency of occurrence, spiny and smooth dogfish sharks are relatively unimportant in the sandbar shark's diet when compared with the importance of skates in the diet (Table 2). Bigelow & Schroeder (1948), Bass et al. (1973), and Lawler (1976) also report the occurrence of shark remains in sandbar shark stomachs. Springer (1960), however, after examining several hundred sandbar sharks from the Florida coast, reported finding very few stomachs with shark remains. The high frequency of occurrence of skates in the sandbar shark's diet can be attributed to their general abundance over the continental shelf (Waring 1986).

Cephalopods From this study, cephalopods (squids and octopus) appear to be generally unimportant in the sandbar shark's diet by evidence of their low number, volume, and frequency of occurrence (Fig. 2). Earlier studies by Springer (1960), Clark & von Schmidt (1965), Lawler (1976), and Branstetter (1981) also showed low occurrences of squid in the sandbar shark's diet, but all were based on specimens obtained from inshore areas of low squid abundance. Our findings, however, suggest that predation on this food source is

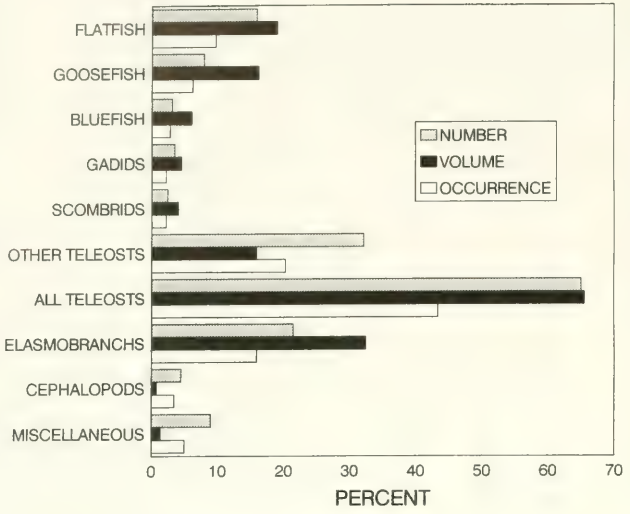

Figure 2

Major food categories consumed by 321 juvenile and adult sandbar sharks *Carcharhinus plumbeus* from the U.S. northeast coast, 1972–84.

probably linked to prey density, since 7 of the 11 stomachs containing squid were from sharks captured offshore where squid are most abundant. It is also possible that the four sharks captured nearshore with squid in their stomachs had moved inshore after eating the squid.

Areal comparisons Flatfish and cephalopods were the only food groups to show significant differences ($P<0.05$, χ^2 test) in importance between the areas. Flatfish occurred most often in nearshore stomach samples, probably as a result of their high summer abundance in shoaler waters along the coast (Bigelow & Schroeder 1953). Cephalopods occurred more often in stomachs offshore because of their high abundance off the U.S. northeast coast (Lange & Sissenwine 1980, Lange 1982), and hence their availability probably accounts for their appearance in the stomachs examined in this study.

Nearshore there was significantly ($P<0.05$, χ^2 test) more predation on elasmobranchs and goosefish by female sharks than by males. Offshore, juvenile males consumed significantly ($P<0.05$, χ^2 test) more 'Other Teleosts' than females. 'Other Teleosts' was the only food group in this area for which there was a difference between sexes. Overall, there was no difference in predation rates on the major food groups with respect to shark size (juveniles or adults).

Food volumes Overall, 49% of examined stomachs contained food. Wass (1973) found that 45% of stomachs from sandbar sharks captured by hook-and-line off Hawaii contained food remains. In other studies, averages have been lower, but up to 29% have been observed for the sandbar shark (Springer 1960, Bass et al. 1973, Lawler 1976).

Our findings show that stomach content volumes ranged from trace amounts to a maximum of 3102 mL, with a mean of 144 mL. The mean for adults was 175.4 mL and 125.2 mL for juveniles. Stomachs from adult and juvenile females contained more food (184.0 and 165.0 mL) on the average than their male counterparts (125.0 and 97.0 mL); however, differences were not significant at the $\alpha=0.05$ level (t-test).

The ratio of stomach content volume to mean body weight ($\bar{x}$BW) varied between different groups of the population, from a low of 0.30% for adult males to a high of 0.83% for juvenile males offshore. The mean for adults and juveniles was 0.33% and 0.55%, respectively, with an overall sample mean of 0.42%. Means for adults of both sexes were similar for the whole sample and nearshore, ranging from 0.30 to 0.36%. Juvenile males and females from nearshore differed the most, with percentages of 0.42 and 0.66, respectively. The highest stomach content values were from an adult and a juvenile female. Stomach contents in these sharks amounted to 5.35 and 5.34% of their body weight, respectively. The adult's stomach contained a whole smooth dogfish and gadid remains. The stomach from the juvenile contained 10 yellowtail flounder *Limanda ferruginea* and a small goosefish. The flounders ($\bar{x}$ size=13.4 cm) may have been consumed as natural prey or obtained as culls from a trawl catch. However, other sandbar sharks caught in the area on the same day contained only 1 or 2 flounder, suggesting that this juvenile female was more successful in obtaining natural prey.

Overall mean stomach volume in terms of liquid capacity for the sharks in this study was 2.62 L which was 7.7% of the $\bar{x}$BW (34.0 kg). For adults, the mean was 5.15 L, amounting to 10.0% of their $\bar{x}$BW (52.3 kg).

A measure of stomach fullness was determined by calculating the ratios of food volume to maximum liquid capacity. The mean food volume (144 mL) was 5.5% of the mean maximum capacity. Dividing the sample by size-class showed that the percent stomach fullness was 5.2 and 13.5 for adults and juveniles, respectively. One stomach from a juvenile female was filled to 50.0% capacity, while two others approximated 40.0%. Just over half (53.0%) of the stomachs contained less than 10.0%. All adults had less than 10.0%, except for two that ranged from 15.0 to 19.0%.

Chincoteague Bay sample

The Chincoteague sample was composed of pups and young juvenile sandbar sharks captured at six fishing stations located in the lower bay estuaries. The overall mean fork length and body weight for these sharks was 55 cm and 1.72 kg, respectively. The mean for 65 newborn pups (39 males, 26 females) was 50.7 cm and 1.38 kg, while the mean for 29 (16 males, 13 females) "older" pups and small juveniles was 63.7 cm and 2.48 kg. There was no difference in mean fork length or body weight between the sexes within each size-class.

Food analysis Food items consisted of crustaceans and fish. By frequency of occurrence, these contributed 82.0 and 13.8%, respectively. Crustaceans were represented primarily by soft blue crabs (75.5%), with the remainder (6.3%) consisting of lady crabs and mantis shrimp. Fish prey consisted of small flounder, anchovy, Atlantic silver sides, mullet, and one smooth dogfish (48 cmTL) eaten in three pieces. A more complete prey list for young sandbar sharks captured in Chincoteague Bay during the summer of 1983 is given in Medved et al. (1985). Previous studies of young sandbar sharks along the Virginia coast also showed that their diets consisted of small fish and crustaceans but was dominated by soft blue crabs (Hoese 1962, Medved & Marshall 1981; V.J. Lascara, Jonathan Corp., Norfolk VA, pers. commun. 1987).

Food volumes Stomachs from 75 (79.8%) sharks contained food varying from trace amounts to a maximum of 125 mL. Nineteen stomachs (20.2%) were empty. Stomachs from 236 sharks caught by gillnets in Chincoteague Bay during the same time-period (Medved et al. 1985) showed that 85.6% (202) held food remains, while 14.4% (34) were empty.

The mean food volume for sharks considered to be newborn pups was 16.6 mL (1.2% of $\bar{x}$BW); for "older" pups and small juveniles, it was 27.0 mL (1.1% of $\bar{x}$BW). The whole sample mean was 20.0 mL or 1.2% of the $\bar{x}$BW.

Estimates of daily ration and annual food consumption

Daily ration Reviews are available of studies and techniques for determining stomach evacuation rates (Windell 1978, Fange & Grove 1979) and daily ration (Davis & Warren 1971, Conover 1978, Mann 1978) for several species of teleosts. Comparable types of studies for sharks are lacking in the literature, primarily because the technology for maintaining sharks in a healthy "normal" condition in the laboratory has not been perfected (Gruber & Keyes 1981). A few excep-

Table 5

A comparison of feeding-related variables for sandbar shark pups *Carcharhinus plumbeus*, and juveniles and adults caught by different gear types in Chincoteague Bay and in the nearshore (<100 m) and offshore (>100 m) waters of the U.S. northeast coast, 1972–84.

				$\bar{x}$ Stomach contents		$\bar{x}$ Meal size		Est. daily ration		
	N	Capture method	$\bar{x}$ BW[a] (kg)	(g)	% of $\bar{x}$ BW	(g)	% of $\bar{x}$ BW	(g)	% of $\bar{x}$ BW	Source
Pups	236	GN[b]	1.88	18.9	0.96	79.5	4.23	20.1	1.07	Medved 1985, Medved et al. (1988)
Pups	94	ST	1.72	20.0	1.16			24.4	1.43	This study
Juveniles and adults	321	ST&LL	34.0	144.0	0.42			293.0	0.86	This study

[a]BW = body weight.
[b]GN = gill net, ST = sport tackle, LL = longline.

tions do exist, however. These include food consumption studies for the lemon shark *Negaprion brevirostris* by Graeber (1974), Gruber (1982), and Longval et al. (1982); digestion rates in the blue shark *Prionace glauca* by Tricas (1977); stomach evacuation and food consumption experiments by Jones & Geen (1977) on the spiny dogfish and Cortés & Gruber (1990) on the lemon shark; stomach evacuation rates in captive sandbar sharks by Wass (1973); and stomach evacuation, food consumption, and daily ration estimates in the sandbar shark by Medved (1985) and Medved et al. (1985, 1988). The data for the last three papers came from experiments conducted on pups and small juvenile sandbar sharks maintained in a natural enclosure in Chincoteague Bay, Virginia. Knowing the rate of gastric evacuation is necessary for determining the daily ration of a species. A number of factors, both biological and physical, influence the evacuation rate in fish (Langton 1977), but temperature, food type, and predator size appear to have the greatest impact (Windell 1966 and 1968, Pandian 1967, Edwards 1971, Jones & Geen 1977, MacDonald et al. 1982, Medved et al. 1985). Jones & Geen (1977) maintained spiny dogfish in aquaria at about 10°C and found that 5 d were required to evacuate a meal of herring. At the same temperature, mature males required 10 d to evacuate a full stomach of herring, and the time required was probably influenced by the size of the dogfish. Wass (1973) found that sandbar sharks (95–101 cm caudal length) maintained in large experimental ponds (temperature unknown) required at least 2–3 d to evacuate their stomachs. In the natural environment around the Hawaiian Islands where surface-water temperatures average about 26°C, he suggested that 3–4+ d might be needed, depending on whether the prey was soft or hard and resistant to digestive enzymes.

Prior to the feeding study, the sharks were starved for 4 d. What effect this had on their gastric evacuation rate is unknown, but studies conducted on various species of teleosts starved before feeding resulted in slower evacuation rates (Windell 1967, Elliott 1972, Jones 1974). Medved et al. (1985) were able to demonstrate the variability in gastric evacuation rates that can occur between food types. Soft blue crabs and Atlantic menhaden *Brevoortia tyrannus* required 70.7 and 92.7 h, respectively, (81.5 h avg.) to be depleted to 98% of their original weight. The difference in depletion time was probably the result of a combination of factors, including a natural lag phase in initial enzyme action on the food items (Jennings 1972) and the resistance of the skin and scales of the fish prey to digestion (Windell 1967, Western 1971). Jobling (1987) also reported that the different surface-to-volume ratio of the two food types and their differing friability will affect gastric evacuation. In addition, a concentration of fat in some fish flesh, such as found in menhaden (Thayer et al. 1973), has been shown to delay gastric evacuation (Quigley & Meschan 1941, Windell 1967, Windell et al. 1969).

In the present study, two approaches were used to estimate daily ration. The first was by use of a calculated routine metabolic rate, and the second was the basic energy equation of Winberg (1956),

$$C = 1.37\,(R+G),$$

where C = energy of food consumed, R = total energy of metabolism, G = metabolic energy in terms of growth, and the coefficient 1.37 represents the 27% of food energy lost through excretion (Brett & Groves 1979). This is a more recent and accurate value than the 20% originally proposed by Winberg (1956).

A metabolic rate for the sandbar shark has not been determined. For our purposes, therefore, we assumed that a routine metabolic rate of 49.2 $mgO_2/kg \times h$ at 10°C for the spiny dogfish (Brett & Blackburn 1978) was appropriate for the sandbar shark. Adjusting for an increase in temperature to 18.5°C (J.C. Casey, Narragansett Lab., NMFS Northeast Fish. Sci. Cent., unpubl. longline data) and using a Q_{10} of 2.2, we derived a metabolic rate of 95.9 $mgO_2/kg \times h$. Using an oxycalorific equivalent of 3.25 cal/mgO_2 cited for fishes (Elliott & Davison 1975), the routine metabolic expenditure is 311.7 $cal/kg \times h$ or 7.48 $kcal/kg \times d$. The average sandbar shark at 34.0 kg BW would thus require 254.3 kcal/d. To compensate for the food energy lost through excretion, the sharks would have to consume 10.2 (7.48×1.37) $kcal/kg \times d$. This would raise the total daily average intake to 346.8 kcal/d (10.2 × 34.0). If we consider the average caloric value of the foods eaten to be 1.195 kcal/g (Steimle & Terranova 1985), the energy intake in terms of food mass amounts to 290.2 g/d (346.8/1.195) or 0.85% of average body weight (BW). Yearly, this amounts to 105.9 kg ($3.1 \times \bar{x}$BW).

To employ the Winberg (1956) energy equation, we calculated a value for G based on an average growth in weight estimate of 3.72 g/d for juveniles and adults (Casey & Natanson 1992). Using an average calorific value of shark flesh of 1.01 kcal/g (Sidwell et al. 1974), the daily increase in caloric content due to growth is 3.75 kcal/d (3.72×1.01). Substituting the energy values for metabolism and growth in the equation gives an energy value for food consumed of 353.5 kcal/d (1.37[254.3+3.75]) or 295.8 g/d (food energy = 1.195 kcal/g). Daily ration then is equal to 0.87% of BW/d and 3.2 × BW/yr.

To estimate daily ration for the sandbar pups from Chincoteague Bay, we assumed the metabolic rate above for the spiny dogfish was appropriate. Correct-

ing for temperature (25.0°C) and using a Q_{10} of 2.2 resulted in a metabolic rate of 160.4 $mgO_2/kg \times h$. When converted to calories, the routine metabolic expenditure is 521.3 cal/kg × h (160.4×3.25), or 12.5 kcal/kg × d. At this rate, the average sandbar pup (1.7 kg) in this study would require 21.2 kcal/d (12.5×1.7) for metabolic needs. When we consider the 27% of food energy lost through excretion, the daily ration would have to provide 17.1 kcal/kg × d (12.5×1.37) or 29.0 kcal/d (17.1×1.7) for the average pup.

Using a caloric value of 1.235 kcal/g for the foods consumed by sandbar pups (Medved et al. 1988), the daily ration required for routine metabolic needs would be 23.4 g/d (29.0/1.235). This is equivalent to 1.38% of the average BW and amounts to 5.0 times the average BW per year.

Daily growth in weight for sandbar pups was determined to be 1.74 g/d. This was based on the reexamination of existing age data and newly collected information by Casey & Natanson (1992). This amount of daily growth in weight is equivalent to 1.75 kcal/d assuming an average caloric value of 1.01 kcal/g for shark flesh (Sidwell et al. 1974). Substituting for metabolism and growth in the Winberg equation gives an energy value for food consumed of 31.4 kcal/d (1.37[21.2×1.75]). Taking the average caloric value of the food eaten to be 1.235 kcal/g, the daily ration would be 25.4 g/d (31.4/1.235) to meet the energy needs for routine metabolic expenditure. This is equivalent to 1.49% of the average BW and 5.4 times the average BW per year. Our average estimate of daily ration (1.43% BW) for sandbar pups above is in very close agreement to the 1.1% determined by Medved et al. (1988).

The validity of using the metabolic rate of one species for another is questionable and is especially so if the original rate is determined by laboratory studies and then extrapolated to studies in the wild. Not only could significant differences exist between species, but routine metabolic energy expended in the wild may be considerably less than that expended under experimental conditions. For instance, Medved et al. (1988) have shown that a large proportion of sandbar shark movement in Chincoteague Bay is accomplished by passively drifting with the currents. This behavior is most likely a way to increase energy efficiency, since locomotion is metabolically costly for fish (Brett & Groves 1979). No doubt there are other ways by which sharks conserve energy in the wild. With the limitations imposed by available data and literature values, we feel our daily ration estimates are reasonable and comparable with estimates for large sharks in other studies (Table 6). When reliable information specific to the metabolic rate of juvenile and adult sandbar sharks is available, better estimates may be possible.

Annual food consumption Estimates of annual food consumption indicated that the pups can ingest 5.2 times their average body weight in a year. The combined juveniles and adults, by comparison, will consume 3 times their average BW annually (Table 6). The gradual reduction in annual food consumption per kilogram of body weight is a normal result of increasing size. Brett & Groves (1979) show that at a young stage, the rate at which fish generally accumulate body mass exceeds the metabolic energy needs for maintenance. Both rates are relatively high initially, but with

Table 6

Comparison of daily ration and annual food consumption estimates for sandbar sharks *Carcharhinus plumbeus* in this study and for six other species of large sharks. BW = body weight.

Species	$\bar{x}$ length (cm)	$\bar{x}$ weight (kg)	kg/d	kg/yr	%BW/d	$\bar{x}$ BW/yr	Source
Mako *Isurus oxyrinchus*	175	63.0	2.000	730.0	3.2	11.6	Stillwell & Kohler (1982)
Lemon *Negaprion brevirostris*	70				3.0		Gruber (1982)
Lemon		2.4	0.020		2.0		Cortés & Gruber (1990)
Lemon	IMMATURE				1.4		Clark (1963)
Lemon	274				0.5		Clark (1963)
Scalloped hammerhead *Sphyrna lewini*		49.9	0.680	248.2	1.4	5.0	Clark (1963)
Blue *Prionace glauca*	187	48.6	0.276	100.7	0.6	2.1	Kohler (1987)
Nurse *Ginglymostoma cirratum*		152.4	0.450	164.3	0.3	1.1	Clark (1963)
Sand tiger *Odontaspis taurus*	137		0.680	248.2			Clark (1963)
Sandbar (juv.)		32.8	0.143	52.2	0.3–0.5	1.6	G. Early*
Sandbar (pups)	56	1.8	0.020	7.3	1.1	3.8	Medved et al. (1988)
Sandbar (pups)	55	1.7	0.024	8.7	1.4	5.1	This study
Sandbar (juv. & adults)	144	34.0	0.293	107.0	0.86	3.1	This study

*New England Aquarium, Central Wharf, Boston MA 02110 (1979).

increasing size and age they decrease at different declining slopes, until, eventually, large mature fish are eating for maintenance and gonad development only. In addition, a reduced capacity to grow may inhibit larger daily intakes of food among older, larger fish (Brett 1971).

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Spatial and temporal occurrence of Spanish mackerel *Scomberomorus maculatus* in Chesapeake Bay*

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The Spanish mackerel *Scomberomorus maculatus* is a pelagic, warm-temperate, or subtropical species that inhabits continental waters from Cape Cod, Massachusetts, south along the Atlantic coast to Florida and through the Gulf of Mexico to the Yucatan Peninsula (Collette et al. 1978, Collette & Russo 1984). In summer, it is considered common along the U.S. east coast north to Chesapeake Bay (Bigelow & Schroeder 1953, Musick 1972). This species was abundant in Chesapeake Bay in the late 1800s, and the most extensive fishery for it in the U.S. occurred there then (Earll 1883). In recent years, Spanish mackerel have again become abundant in Chesapeake Bay (Chittenden et al. In review).

Much work has been done on Spanish mackerel (see Berrien & Finan (1977) and Lukens (1989). However, other than Chittenden et al. (In review), no studies have been directed at this species in the cold-temperate waters north of Cape Hatteras NC, since Ryder (1882) and Earll (1883) over 100 years ago. As a result, little information exists from which to plan collection of basic biological data on this species in the Chesapeake Region, much less to manage it there.

The objectives of the present study are to describe spatial and temporal distributions of Spanish mackerel in Chesapeake Bay using catch estimates from direct observations of catches and interviews of commercial fishermen, and to relate the temporal distribution of this species to water temperature. This basic information is needed to plan other research on this species in the Bay.

Methods

Our data cover the period 1988–90, but primarily 1989, and were obtained from commercial pound-net fisheries that cover a broad area of the Virginia waters of Chesapeake Bay (Fig. 1). The individual Chesapeake Bay fisheries are generally small in scale, usually fishing 1–7 nets in the local waters of each fishery. The nets are usually emptied daily, depending on wind conditions, size of the local catch, and market conditions. Reid (1955) and Chittenden (1991) describe the Chesapeake Bay pound-net fisheries, e.g., gear, fishing, and catch-processing procedures.

We present next our sampling design for 1989, the major period of study. At weekly or fortnightly intervals, we made 51 on-site observations and 66 telephone calls to cooperating fishermen to get daily catch-record information to estimate the size of Spanish mackerel catches at their commercial pound-net fisheries (see Fig. 2 for the spatial and temporal distribution of these data contacts). We studied four fisheries, which were chosen because they were usually cooperative in providing information, were widely-spaced along the Chesapeake Bay, and were among the major fisheries in their areas. These characteristics facilitated data collection, giving the study widespread geographic coverage and pertinence to major portions of the Chesapeake Bay pound-net fishery. Three of the contacted fisheries were located along the 'Western Shore' of Chesapeake Bay (Fig. 1), off (1) Lynnhaven, (2) the lower York River, and (3) Reedville; the fourth was located along the lower 'Eastern Shore' near Kiptopeke. Though not all the nets were emptied every day, in 1989 these fisheries fished 21 pound-nets (Table 1), about 10% of the roughly 200 net licenses issued in the Chesapeake Bay pound-net fishery. The pound-net fisheries begin fishing each year (and our initial contacts were made) well before Spanish mackerel enter Chesapeake Bay; the fisheries continue operating (and our later contacts were made) well after this species leaves the Bay (see the occurrence of zero catches in Fig. 2).

Findings in 1989 were supplemented with information from 1988 and 1990, which was obtained using the same sampling design and procedures as in 1989 but with less regular and extensive contacts. In 1988 contacts were primarily made in the last half of the fishing season; we used this data to describe when Spanish mackerel disap-

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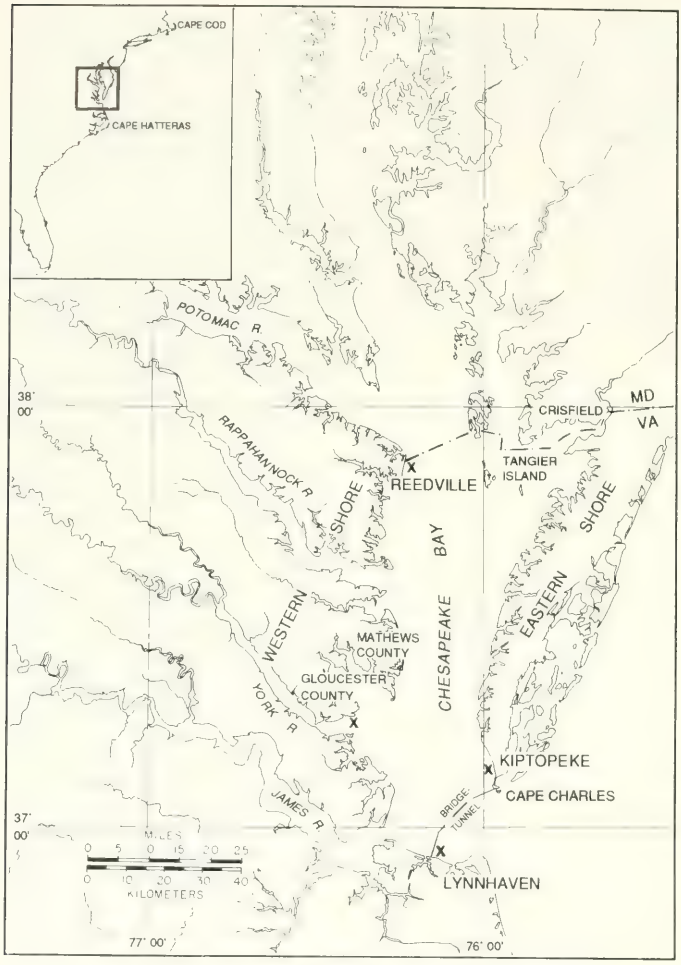

Figure 1
Chesapeake Bay geography. The four fishery locations are indicated by x's.

peared that year. In 1990, contacts were primarily made in the first half of the fishing season; we used that data (Fig. 3) to describe when Spanish mackerel appeared and became abundant that year. Catch-size information for 1989 and 1990 was related to daily surface-water temperature records at Kiptopeke and at the Chesapeake Bay Bridge Tunnel, provided by the National Ocean Survey (Fig. 1).

The accuracy of our estimates of catch size varied from data contact to contact, because the estimates were not always simple catch data. Most estimates were quite accurate, particularly when catches were zero or very small (e.g., records being "none caught," "few caught," etc.), when, as usual, the fishermen were willing to give a specific estimate ("*n* boxes caught"), or when the catch was stacked in boxes on pallets for shipment and could be counted by us. In some cases, our estimates were verbal (e.g., records being "larger than last week," etc.). To compare estimates, the size of the catch from each data contact in 1989 and 1990 was scored in the following categories: (0) no Spanish mackerel caught, (1) <1 22.6 kg box of fish caught, (2) 1–5 boxes, (3) >5–10 boxes, (4) >10–20 boxes, and (5) >20 boxes. Adjacent categories may show some overlap, because the original records are inexact. However, these categories permitted a distinct separation of zero or small catches (categories 0,1) from large catches (categories 3,4,5), but a less-distinct separation of intermediate-sized catches. We feel the error of these estimates is small and does not affect the broad spatial and temporal patterns described.

To evaluate temporal distributions, differences in monthly catches in 1989 were tested for each location using a Kruskal-Wallis one-way nonparametric analysis of variance (Table 1) after ranking the scores (SAS 1988). This was supported by Tukey's multiple comparisons tests (Table 2), applied to the ranked scores to evaluate specific monthly differences. Similar procedures were followed to evaluate spatial distributions. We interpret significance tests on spatial differences with caution, because the number of nets varied among locations and information does not exist to standardize nets and nominal effort. We feel this has little

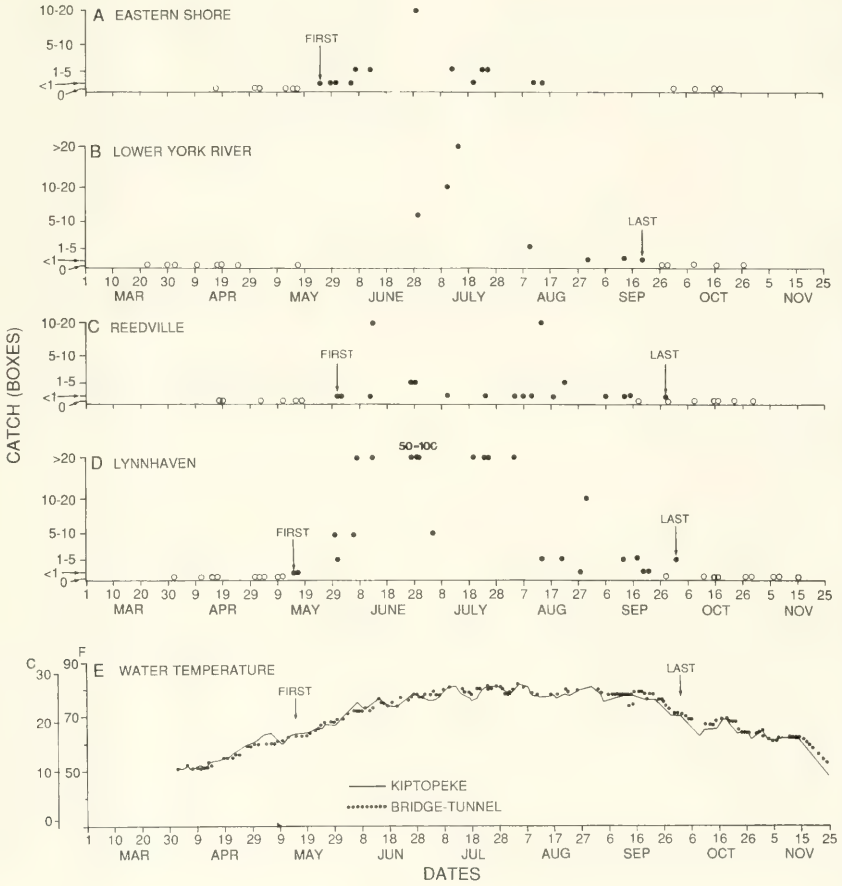

Figure 2

Estimates of daily Spanish mackerel *Scomberomorus maculatus* catches (no. of 22.6 kg boxes landed) in 1989 in Chesapeake Bay: **(A)** Eastern Shore, **(B)** lower York River, **(C)** Reedville, and **(D)** Lynnhaven, with daily water temperatures **(E)** at Kiptopeke and off the Chesapeake Bay Bridge-Tunnel. All data contacts are indicated. Zero catches are indicated by open circles. One box = 22.6 kg fish. "First" and "Last" indicate dates when first and last fish were captured; this is not specified when a long time-lapse in sampling occurred before the "First" or after the "Last" record.

effect on temporal trends, however, because the same number of nets was generally used in a fishery throughout the season.

To make significance tests for differences between areas, we converted the raw catch records to catch-per-unit-effort (C/f) by using the nominal number of nets (Table 1) to estimate effort. The resulting C/f records were then scored into the categories described above. This procedure does not change the original scores for records of "no catch" or "<1 box"; it does tend to lower scores for larger catches, thereby making it more difficult to declare significance.

Table 1

Summary, by location, of Kruskal-Wallis one-way nonparametric significance tests for monthly differences in Spanish mackerel *Scomberomorus maculatus* catches in 1989. n = number of records at one location, df+1 = number of months sampled.

Location	Nets	n	χ^2	df	Prob.
Reedville	2	31	21.83	6	0.0013
York River	7	20	16.37	7	0.0219
Lynnhaven	5	43	31.86	7	0.0001
Eastern Shore	7	23	16.94	5	0.0046

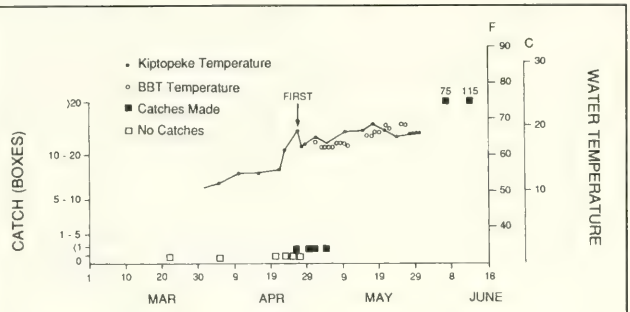

Figure 3

Estimates of daily Spanish mackerel *Scomberomorus maculatus* catches (no. of 22.6 kg boxes landed), early 1990 at Lynnhaven in Chesapeake Bay, with daily surface-water temperatures at Kiptopeke and off the Chesapeake Bay Bridge-Tunnel (BBT). "First" indicates date when first fish were captured. No records collected mid-May to early June.

Table 2

Summary, by location, of Tukey's multiple comparisons tests to evaluate specific monthly differences in Spanish mackerel *Scomberomorus maculatus* catches in 1989. Mean ranks (of scores for catch sizes; see Methods) without the same letters are significantly different at α=0.05.

Month	n	Mean rank	Significance			Month	n	Mean rank	Significance		
Reedville						**York River**					
Jun	5	25.3	a			Jul	2	19.5	a		
Aug	6	23.1	a			Jun	1	18.0	a		
Jul	2	20.0	a	b		Aug	2	16.0	a		
Sep	6	15.7	a	b	c	Sep	4	11.0	a	b	
May	5	9.6		b	c	Mar	2	7.0		b	
Apr	2	7.0			c	Apr	5	7.0		b	
Oct	5	7.0			c	May	1	7.0		b	
						Oct	3	7.0		b	
Lynnhaven						**Eastern Shore**					
Jun	6	36.8	a			Jun	4	19.3	a		
Jul	4	36.3	a			Jul	4	18.5	a	b	
Aug	5	29.1	a	b		Aug	2	14.0	a	b	c
Sep	4	21.1		b	c	May	8	8.7		b	c
May	9	16.7		b	c	Apr	1	5.5			c
Oct	7	12.4			c	Oct	4	5.5			c
Apr	4	10.0			c						
Nov	3	10.0			c						

Spatial distribution

Results

Spanish mackerel become widely distributed in summer throughout Virginia waters of the Chesapeake Bay. In 1989, we observed large catches, at least on occasion, at Lynnhaven, off the lower York River, on the Eastern Shore, and at Reedville (Fig. 2). Catches were consistently large in June, July, and early August off Lynnhaven and apparently off the lower York River, although records were not as complete there. Comparatively low catches were consistently made at Reedville and on the Eastern Shore. We formed the distinct impression from our data and observations that Spanish mackerel were much more abundant in the summer along the lower Western Shore of Chesapeake Bay in 1989 than either along the Eastern Shore or upbay at Reedville.

Our interpretation of spatial patterns in Spanish mackerel abundance is supported by significance tests that evaluate the null hypothesis, within months, of no difference in C/f between areas. Kruskal-Wallis non-parametric tests for 1989 showed significant differences in C/f between areas in June and July (Fig. 4), when peak abundance occurred, but there were no significant differences in the other months when abundance was lower (Table 3). Tukey's multiple comparisons tests (Table 4) showed significantly higher C/f in July at Lynnhaven and the lower York River than at Reedville or the Eastern Shore. In June, these tests showed significantly higher C/f at Lynnhaven than on the Eastern Shore. Reedville C/f in June was intermediate and not significantly different from either Lynnhaven or the Eastern Shore; data from the Lower York River were not included in the Tukey's test presented because only one data contact was made there in June.

Discussion

Spanish mackerel primarily occur in the lower Chesapeake Bay, i.e.,

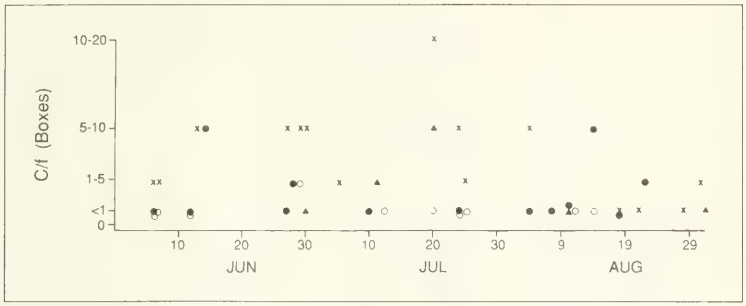

Figure 4
Estimates of daily Spanish mackerel *Scomberomorus maculatus* catch-per-unit-effort (C/f, no. of 22.6 kg boxes landed), June–August 1989 by location. Comparatively few or no fish were landed March–May and September–November. (x) Lynnhaven, (▲) lower York River, (●) Reedville, (○) Eastern Shore.

Table 3
Summary, by month, of Kruskal-Wallis one-way nonparametric significance tests for differences between areas in Spanish mackerel *Scomberomorus maculatus* catches in 1989. n = number of records in one month, df+1 = number of areas.

Month	n	χ^2	df	Prob.
Apr	12		none caught	
May	23	1.51	3	0.6799
Jun	16	8.34	3	0.0395
Jul	12	9.68	3	0.0215
Aug	15	1.86	3	0.6011
Sep	14	0.53	2	0.7673
Oct	19	1.71	3	0.6338

Table 4
Summary, by month, of Tukey's multiple comparisons tests to evaluate specific differences between areas in Spanish mackerel *Scomberomorus maculatus* catches in 1989. Mean ranks (of scores for catch-per-unit-effort, see Methods) without the same letters are significantly different at $\alpha=0.05$. There were no significant differences in months not tabulated.

Area	n	Mean rank	Significance	
June				
Lynnhaven	6	11.50	a	
Reedville	5	6.40	a	b
Eastern Shore	4	4.75		b
July				
Lynnhaven	4	9.63	a	
York River	2	9.25	a	
Reedville	2	3.50		b
Eastern Shore	4	3.50		b

the waters of Virginia. We found regular occurrences at Reedville near the Potomac River mouth, occasionally in high numbers as noted by Uhler & Lugger (1876), although Hildebrand & Schroeder (1928) reported few occurrences north of the Rappahannock River. Many fish may enter Maryland waters in years of abundance (Butz & Mansueti 1962), such as in 1880 when landings were 8.2 t (Earll 1883). However, catches there have always been small compared with those in Virginia, where landings made up 97–99% of the reported bay-wide catch in 1880 (Earll 1883), in 1920 (Hildebrand & Schroeder 1928), in 1887–1967 (Lyles 1969), and in 1968–76 (Trent & Anthony 1979), and in 1978–90 (from annual printouts, "(*Year*) landings for the U.S.," provided by the NMFS Office of Data Information Management to VIMS library).

Spanish mackerel may be abundant throughout much of the Chesapeake Bay in Virginia. Large pound and gillnet fisheries existed for it in the 1880s off Gloucester and Mathews counties on the Western Shore, off the Eastern Shore from Cape Charles to Crisfield MD, and off Tangier Island VA (Earll 1883 and 1887, McDonald 1887). Fish also enter the more-saline, lower parts of tributaries like the Potomac and York Rivers (Baird cited in Goode 1888, Hildebrand & Schroeder 1928).

Though they may be useful for management and environmental impact assessment, little data exist to describe in fine detail the spatial distribution of Spanish mackerel in Chesapeake Bay. Such data would be difficult and probably expensive to obtain without mandatory catch-reporting by all the commercial fisheries, because this is a pelagic, fast-swimming, and widely-distributed species that is not well suited to most fishery-independent collecting programs. However, the large-scale distributional patterns of this species apparently have been stable for over 100 years. Our data, biological notes, and anecdotal information from the years 1870–80 (Uhler & Lugger 1876, Earll 1883 and 1887, McDonald 1887) and 1920–60 (Hildebrand & Schroeder 1928, Butz & Mansueti 1962), and long-term landings data from Maryland and Virginia indicate that this species primarily occupies waters which, according to Lippson & Lippson (1984), are of polyhaline salinity (18–30 ppt) and the saltier portions of mesohaline waters (5–18 ppt).

Temporal distribution

Results

Spanish mackerel occur in Chesapeake Bay from late April to early October. They first appeared in the catches on 15 May 1989 (Fig. 2) when three fish were taken off Lynnhaven, on 26 April 1990 (Fig. 3) when two fish were taken there, and, anecdotally according to those fishermen, on about 10 May 1991. Though fishing continued well afterwards, the last catches were on 3 October 1988 and 2 October 1989, dates when we recorded only a few individuals at the lower York River and Lynnhaven fisheries, respectively.

Peak abundance of Spanish mackerel in Chesapeake Bay occurs from early or mid-June through mid-August, based on pound-net records. After the first appearance in 1989, catches at Lynnhaven rapidly rose to high levels in early to mid-June and remained high through mid- to late August (Fig. 2). Combined catches at Reedville, the lower York River, and the Eastern Shore showed the same pattern. Comparatively few fish were captured in any area after late August or early September in that year. After fish appeared in late April 1990, catches at Lynnhaven remained low through at least early May (Fig. 3) when our observations temporarily ceased. Catches were large at Lynnhaven by early to mid-June when observations were made again.

Our interpretation of temporal patterns in Spanish mackerel abundance is supported by significance tests that evaluate the null hypothesis of no difference in catch between months within locations. Significant differences in catch were found between months at each location in 1989 (Table 1). Catches were significantly higher at each location in summer months (June, July, August) than in early spring (March, April) or late fall (October, November) (Table 2). As typically occurs with multiple comparisons tests, intermediate-size catches in May and September were or were not significantly different from adjacent periods of higher or lower catch; the trend of increasing abundance to midsummer and decreasing abundance into fall is the most important feature here.

Spanish mackerel abundance during the season follows a unimodal pattern. Catches in 1989 at Lynnhaven especially, along the Eastern Shore, and off the lower York River show a roughly bell-shaped distribution (Fig. 2). Catches may be bimodal at Reedville near the upbay margin of the range.

Spanish mackerel occur in Chesapeake Bay when water temperatures near the Bay mouth exceed about 17°C. The first fish were taken at Lynnhaven when temperatures had risen to 17°C in 1989 (Fig. 2), and, in 1990, 19°C after a period of rapid temperature increase in late April (Fig. 3). Large catches began in late May in 1989, soon after temperatures rose to 20°C (Fig. 2), and catches remained large through midsummer at 21–27°C. The last fish were taken at Lynnhaven on 2 October 1989 when temperatures decreased and remained below 21°C.

Discussion

Our data on the temporal occurrence of Spanish mackerel in Chesapeake Bay agree with Earll (1883) and Hildebrand & Schroeder (1928) in that (1) the overall period of occurrence in this species is generally mid-May through early October, (2) peak abundance is early June through mid-August or mid-September, (3) the last records of catches are all in early October, and (4) the initial records of appearance are generally in mid-May (10, 15 May in our records; 12, 20 May in previous records), though fish may appear considerably earlier (26 April, our records). Our late-April record may reflect the early, rapid temperature increase that occurred in 1990. The period when Spanish mackerel occur in Chesapeake Bay is shorter than their late-April to early-November distribution off North Carolina (Earll 1883, Smith 1907, Roelofs 1951) but is somewhat longer than their distribution off New York and New Jersey, variously reported as late May or late July to late September–early October (Earll 1883, Bean 1903, Nichols & Breder 1926). The bell-shaped distribution of catches that we, and apparently Hildebrand & Schroeder (1928), observed for Chesapeake Bay differs from a bimodal distribution (i.e., peak abundance in spring and fall) reported for North Carolina (Smith 1907, Hildebrand & Cable 1938, Roelofs 1951). Presumably, this reflects a north-south migration by part of the population(s) through North Carolina waters in spring and fall, in contrast to a summer residence in the Chesapeake.

Munro (1943) reported that the genus *Scomberomorus* is subtropical and tropical in distribution, the optimum range of all species being within the 20°C ocean isotherm in summer. Our findings agree, in that Spanish mackerel initially appear in Chesapeake Bay at temperatures of about 17-19°C and become abundant at about 20°C. Other reports also support that value (Earll 1883, Manooch 1984, Goode 1888). Perret et al. (1971) captured one fish at 10°C, but that appears unusual. Beaumariage (1970) related the 20°C ocean isotherm to Spanish mackerel distribution and suggested Long Island would be near their northern limit in August. Indeed, they are uncommon off Massachusetts (Nichols & Breder 1926, Bigelow & Schroeder 1953). The time-period when temperatures are above 20°C decreases with increasing latitude, and

that probably explains why, as noted above, this species occurs for respectively shorter periods in the summer off New Jersey-New York, in Chesapeake Bay, and off North Carolina.

Timing of the appearance and disappearance of Spanish mackerel in Chesapeake Bay is probably regulated, in part, by temperature differences between the Bay and ocean. Bay waters warm up faster than the ocean in spring and cool faster in fall, due to their different volumes. Cooler ocean temperatures probably limit the time when fish arrive in Chesapeake Bay in spring, and cooler Bay temperatures probably limit the length of time they remain there in fall. Ocean isotherms off the Bay mouth in May and September–October show slightly warmer water along the southern (e.g., Western) shore of the Bay (Anonymous 1989a,b,c). In spring, this might encourage fish to initially enter the Bay along the Western Shore as our records suggest. In fall, it might encourage them to leave that area last.

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Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae)

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Slow-growing fish tend to have heavier, larger otoliths than fast-growing fish of the same length, because otoliths continue to grow even when somatic growth has slowed or stopped (e.g., Templeman & Squires 1956, Mosegaard et al. 1988, Reznick et al. 1989, Secor & Dean 1989, Secor et al. 1989, Campana 1990, Pawson 1990). This uncoupling has important implications for the back-calculation of fish lengths from check marks in the otoliths. If the relationship between an otolith dimension and fish length varies with growth rate, the back-calculated lengths may be biased (Campana 1990). This bias may be largely overcome by specifying a "biological intercept" (such as otolith and somatic size-at-hatching) and incorporating time-varying growth (as measured by daily increment widths) into the back-calculation equation (Campana 1990).

Pagrus auratus (Bloch & Schneider 1801) is a commercially-important sparid fish that ranges through most of the temperate to subtropical Western Pacific Ocean (Paulin 1990). It has been reported previously under a variety of synonyms, especially *P. major* (Japan), *Chrysophrys auratus* (Australia and New Zealand), and *C. unicolor* (Australia) (Paulin 1990). The common name for *P. auratus* in New Zealand and Australia is "snapper," though it is not a true snapper (Lutjanidae).

Uncoupling of otolith and somatic growth has been demonstrated in reared larval and presettlement juvenile *P. auratus* from Japan (Secor et al. 1989). In this study, we report uncoupling of otolith and somatic growth in wild, post-settlement, juvenile New Zealand snapper. We also discuss the implications this has for back-calculation of juvenile snapper lengths using otolith daily increments.

Methods

Snapper were caught using a small otter trawl net equipped with a 20 mm stretched-mesh codend. Samples were collected near Kawau Island, Hauraki Gulf, New Zealand (36°25'S, 174°46'E), January 1987 to March 1989. Fish were chilled on capture, and frozen within 24 h. After thawing, snapper were measured to the nearest mm fork length (FL). Trial measurements before and after freezing and thawing showed that shrinkage was minimal (mean shrinkage=2.03%, SD=1.09%, n=42), thus no length corrections were made.

In New Zealand, snapper have a prolonged summer spawning season from October to February (Scott & Pankhurst 1992), and we follow Paul (1976) in taking the theoretical birthday as 1 January. Each year-class was numbered after its first full year; e.g., snapper spawned during the 1986–87 austral summer were assigned to the 1987 year-class. Age-0+ fish were identified from length-frequency modes; they grow to about 80–140 mmFL at the end of their first year (Paul 1976; M.P. Francis, unpubl. data).

Sagittae were removed, and one of each pair was weighed and measured for maximum length (anterio-posterior axis) and height (dorso-ventral axis). For snapper <200 mmFL, transverse sections[1] were prepared from a subsample of sagittae, and sulcal width was measured as the distance between the sulcal side of the metamorphic mark (Francis et al. In press) and the sagitta margin at the ventral edge of the sulcus. This measurement was used in preference to total sagitta width because the antisulcal face of sagittae varied considerably in shape, making it a poor reference surface, and because most of the increase in sagitta width occurred on the sulcal surface. The collective term "size variables" is used here when referring to sagitta weight, length, height, and sulcal width.

A series of analyses of covariance (ANCOVA) were used to investigate the effects of year-class (1987 and 1988) and seven sampling periods (Table 1) on the relationship between the four size-variables and FL in 0+ snapper.

Data from snapper samples collected in Periods 2 and 3 (Table 1) were used to determine whether sagitta size at any given FL depends

[1]Terminology used to describe otolith planes and ageing follows Wilson et al. (1987).

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Table 1

Sampling periods for age-0+ snapper *Pagrus auratus*, 1987 and 1988 year-classes.

Period	1987	1988
1	27 January	4 February
2	2 March	15 March
3	28 April	6 April
4	30 June	30 May–7 June
5	24–27 August	25 July–4 August
6	19 October	31 October
7	14 December	29 Nov–20 Dec

on somatic growth rate. Regressions were fitted to plots of size-variables vs. FL, and the residuals were plotted against somatic growth rate. The latter was estimated by the equation

Somatic growth rate = (FL–8)/(post-metamorphic age),

where the constant 8 represents approximate mean length of snapper at metamorphosis (Fukuhara 1985 and 1991, Foscarini 1988, Battaglene & Talbot 1992). Post-metamorphic age-at-capture was estimated from transverse sections by counting daily increments between the metamorphic mark and the section margin (see Francis et al. [In press] for validation of daily increments). Post-metamorphic age was used rather than post-hatch age because only about 10% of our sections contained cores; use of post-hatch age would have severely limited sample sizes. Similar analyses were not performed on data from Period 1 because of small sample size, nor on data from Periods 4–7 because daily increments deposited during winter are not resolvable with a light microscope (Francis et al. In press).

Results

Figure 1 shows plots of sagitta size-variables vs. FL for all sampling periods and age-classes combined. Sagitta weight increased exponentially with FL (Fig. 1A). Plots of sagitta length, height, and sulcal width vs. FL were convex, with slopes decreasing over the range 35–300 mmFL (Fig. 1B).

Data for 0+ snapper of the 1987 and 1988 year-classes collected in Periods 1–7 were extracted for further analysis by ANCOVA. Because only linear relationships can be analyzed by ANCOVA, sagitta weight and FL were $\log_{10}$ transformed before the relationship between them was analyzed. Relationships between the other three size-variables and FL are clearly

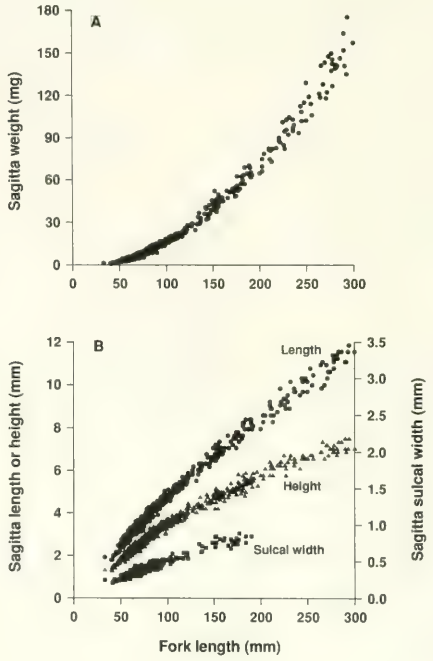

Figure 1

Plots of **(A)** sagitta weight vs. fork length, and **(B)** sagitta length, height, and sulcal width vs. fork length for *Pagrus auratus*. Data for all sampling periods and age-classes combined.

nonlinear (Fig. 1B). However, ANCOVAs fit linear regressions to individual samples (i.e., sagittae of snapper from one year-class caught in one period), which span only short segments of the lower end of the FL range shown in Fig. 1B. All samples were tested for nonlinearity by regressing size-variables against FL, and plotting the residuals against FL. There were no trends in the residuals, so the untransformed data were used in the ANCOVAs.

The first set of four ANCOVAs (one for each size-variable) tested the effects of year-class and sampling period on sagitta size, using FL (or $\log_{10}$FL) as the covariate. There were no significant interaction terms involving year-class, and the year-class factor itself was not significant ($p>0.05$) in any ANCOVA. Therefore, data for the two year-classes were pooled for subsequent analyses.

A second set of four ANCOVAs tested the effect of the seven sampling periods on sagitta size. In each case, the slopes of the regression lines differed significantly among sampling periods (Table 2). Slope coefficients declined markedly between Periods 4 and 5 (Table 3); consequently, a third set of four ANCOVAs was limited to data for Periods 1–4. Whereas slopes did not differ significantly for sagitta length, height, or sulcal width, the intercepts did (Table 2). The three size-variables increased relative to FL between time-periods, i.e., snapper sampled later in the year had larger sagittae than those sampled earlier (Fig. 2B). The only sample-pairs that did not differ were Periods 1 and 2 for sagitta height and sulcal width measurements (Table 2). In the ANCOVA of sagitta weight vs. FL, slopes differed significantly among the four periods; thus the intercepts could not be tested (Table 2). However, sagitta weight followed the same trend as the other size-variables, being greater in snapper sampled later in the year than in those sampled earlier (Fig. 2A).

Table 2

Summary of results of ANCOVAs of sagitta size-variable data for snapper *Pagrus auratus*, 1987 and 1988 year-classes combined. Separate analyses were performed with the variables length, height, sulcal width, and $\log_{10}$ (weight). The covariate was fork length for the first three analyses and $\log_{10}$ (fork length) for the last. NS = not significant; $^{*}p<0.05$, $^{**}p<0.01$.

Sagitta size-variable	Periods	Test for slope differences	Test for intercept differences	Periods for which intercepts did **not** differ ($p>0.05$)[1]
Length	1–7	` `		
	1–4	NS	**	Nil
Height	1–7	**		
	1–4	NS	**	1 & 2
Width	1–7	*		
	1–4	NS	` `	1 & 2
Log(weight)	1–7	` `		
	1–4	` `		

[1]Conditional Tukey-Kramer test.

Table 3

Regression slopes for the relationships between sagitta size-variables and fork length for snapper *Pagrus auratus* during seven sampling periods. Sagitta length, height, and sulcal width were regressed against fork length, and sagitta $\log_{10}$ (weight) against $\log_{10}$ (fork length). Data for Periods 1–4 are shown in Fig. 2. N = sample size.

	Length		Height		Width		Log(weight)	
Period	N	Slope	N	Slope	N	Slope	N	Slope
1	17	0.045	22	0.032	14	0.0035	18	2.69
2	83	0.042	92	0.031	44	0.0039	88	2.30
3	38	0.040	58	0.033	53	0.0036	40	2.14
4	84	0.041	86	0.033	42	0.0036	83	2.32
5	61	0.037	65	0.028	22	0.0033	62	2.08
6	71	0.037	72	0.027	20	0.0027	72	2.05
7	45	0.038	47	0.029	16	0.0024	44	2.12

Periods 2 and 3 data were used independently to investigate the effect of growth rate on size-variables **within** sampling periods. The data represent juveniles with estimated post-metamorphic ages of 53.5–136.0 d, and lengths of 43–96 mm FL. Estimated growth rates, averaged over the whole juvenile life, ranged from 0.54 to 0.93 mm/d. Residuals from regressions of Period-2 size-variables vs. FL were negatively correlated with somatic growth rate (r=–0.87, –0.70, –0.74, and –0.54 for sagitta weight, length, height, and sulcal width, respectively; $p<0.01$ in all cases). Therefore, sagittae were heavier and larger (in all dimensions) in slow-growing than in fast-growing snapper. Sagitta weight residuals are plotted against growth rate in Fig. 3.

Residuals from regressions of Period-3 size-variables vs. FL were also negatively correlated with somatic growth rate (r=0.45, –0.39, –0.13, and –0.26 for sagitta weight, length, height, and sulcal width, respectively). However, only the sagitta weight correlation was significant ($p<0.05$).

To determine whether differences in somatic growth rate might explain the observed differences in sagitta size variables **between** sample periods (Fig. 2), an analysis of variance was performed on growth-rate estimates for Period-2 and -3 snapper. Variances for the two periods were homogeneous ($F_{46,60}$=1.15, $p>0.05$. Period-2 snapper had significantly higher growth rates ($\bar{x}$ 0.81 mm/d, range 0.68–0.94 mm/d) than Period-3 snapper ($\bar{x}$ 0.66 mm/d, range 0.55–0.82 mm/d, $F_{1,106}$=128.0, $p<0.001$).

Discussion

Residuals analysis showed that in Period 2 and over the length range 43–90 mmFL, slow-growing snapper had larger sagittae (relative to FL) than fast-growing snapper. In Period 3, a similar but weaker pattern was found. This study, therefore, demonstrates uncoupling of sagitta and somatic growth in wild age-0+ snapper, and extends a previous report of such uncoupling in reared Japanese snapper up to 30 mmSL (Secor et al. 1989).

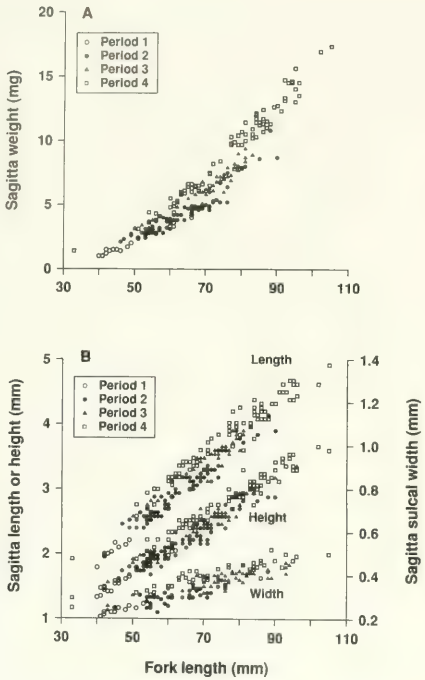

Figure 2

Plots of **(A)** sagitta weight vs. fork length, and **(B)** sagitta length, height, and sulcal width vs. fork length for age-0+ *Pagrus auratus*, 1987 and 1988 year-classes, sampled during Periods 1–4 (see Table 1).

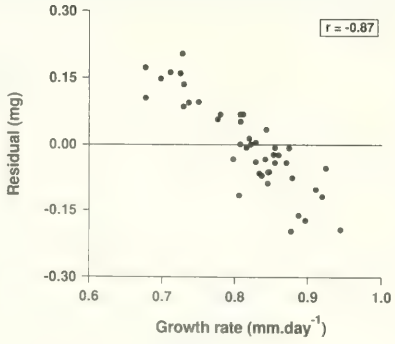

Figure 3

Residuals from a $\log_{10}$ (sagitta weight) vs. $\log_{10}$ (fork length) regression of the Period-2 data from Figure 2A plotted against *Pagrus auratus* post-metamorphic growth rate.

Increases in sagitta size-variables **between** Periods 2 and 3 are also consistent with a growth rate effect: snapper with lower growth rates (Period 3) had larger sagittae than those with higher growth rates (Period 2). Snapper growth rate generally declines between summer and winter (Paul 1976), so the pattern of increasing sagitta size over Periods 1–4 (summer–winter) is also consistent with a growth-rate effect.

Between Periods 4 and 5, the slopes of single-sample plots of size-variables vs. FL decreased. A reduction in slope during the winter months suggests that somatic growth slows faster in small than in large snapper, leading to relatively larger sagittae in the former. The reduction in slope is responsible for the curvilinear trends observed when data from all periods are pooled (Fig. 1B). A similar effect of season on sagitta-somatic relationships has been reported in other species (Reay 1972, Thomas 1983).

When sagitta and somatic growth rates are uncoupled, back-calculated lengths may be biased (Campana 1990). To reduce this bias, Campana (1990, eq. 4) connected the growth trajectory end-points (i.e., sagitta and somatic sizes-at-capture) with a "biological intercept" (he suggested sagitta and somatic size-at-hatching). Snapper larvae are about 2 mmSL (equivalent to ~2.5 mmFL) at hatching, and have circular sagittae that are 0.010–0.012 mm in diameter (M.P. Francis, unpubl. data). These values would form an appropriate biological intercept for daily increment back-calculations using measurements in either the anterio-posterior (length) or dorso-ventral (height) axes.

Francis (1990) reviewed back-calculation methods, but was not aware of Campana's (1990) study. Francis identified two back-calculation hypotheses: scale (=sagitta) proportional, and body (=somatic) proportional. He pointed out that the commonly used Fraser-Lee equation follows neither hypothesis, and recommended that it be replaced with an equation that does. Campana's equation 4 is a modification of the Fraser-Lee equation, and also does not follow scale- or body-proportional hypotheses. This is easily shown by considering the point at which growth trajectories converge. For scale-proportional methods, this point is on the body-size axis; for body-proportional methods, the point is on the scale-size axis; for Campana's method, the point is at the biological intercept which will usually have some small, positive value on both axes (Campana 1990, Francis 1990). Campana's method, therefore, represents a third back-calculation hypothesis, which is based on the idea that the proportional relationship between scale and body size is initiated at some growth stage, such as hatching. (The Fraser-Lee equation was also based on this idea, but, in practice, most authors using that equation calculated the intercept from a regression line rather than from biological data [Francis 1990]).

The key factor that must be considered when deciding which back-calculation method to use is the accuracy with which it estimates back-calculated lengths. Comparison of mean back-calculated lengths with mean observed lengths can detect only gross errors (Francis 1990), and is not a good test for accuracy. Campana (1990) used simulations to show that his method removed much of the bias associated with a sagitta-somatic growth-rate effect. The existence of a strong growth-rate effect in juvenile snapper suggests that Campana's method should be used to overcome the expected bias.

Campana's (1990) equation 4 corrects for growth-rate variability among fish, while assuming linear sagitta-somatic trajectories for individual fish. The need for the latter assumption can be overcome by incorporating time-varying growth into the model (Campana 1990, eq. 7). However, there are two obstacles to use of the time-varying model for snapper: First, the model takes no account of sagitta and somatic size-at-capture, which limits its use to back-calculation of **mean** lengths; second, the model requires width measurements from all daily increments between the biological intercept and capture, plus a proportional relationship between increment width and somatic growth. For snapper, the relationship between increment width and somatic growth is unknown. Furthermore, recent work on other species has shown that changes in increment width may lag or be unrelated to changes in somatic growth (Molony & Choat 1990, Wright 1991). For these reasons, we recommend that back-calculation of snapper lengths from daily increments be done using Campana's equation 4.

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A new method of oocyte separation and preservation for fish reproduction studies*

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Studies on the reproduction of multiple-spawning fishes often involve estimates of batch fecundity and oocyte size (Hunter & Goldberg 1980, DeMartini & Fountain 1981, Hunter et al. 1985, Brown-Peterson et al. 1988). Because data collection and laboratory analysis are rarely concurrent, oocytes which are preserved and hardened are generally used for these analyses. It is critical, therefore, to have a method of oocyte preservation which does not damage or destroy oocytes and has a determinate effect on oocyte size.

The preferred oocyte preservative (Bagenal & Braum 1978, Snyder 1983, Cailliet et al. 1986) has been a modified Gilson's solution: 100 mL 60% ethanol or methanol, 880 mL water, 15 mL 80% nitric acid, 18 mL glacial acetic acid, and 20 g mercuric chloride (Snyder 1983). The benefit of using Gilson's is its ability to harden oocytes while chemically separating them from ovarian tissue. However, a number of problems are associated with this procedure, including degeneration of hydrated oocytes (Hunter et al. 1985, Schaefer 1987, Brown-Peterson et al. 1988); substantial and continuous oocyte shrinkage, reported to range from 15% to 24% (DeMartini & Fountain 1981, Schaefer 1987, Witthames & Greer Walker 1987); a relatively long fixation period of several days to a few weeks (Cailliet et al. 1986); and the extreme toxicity of mercuric chloride (West 1990).

Formalin solution (4–10%) has also been used to preserve whole fish ovaries (Bagenal & Braum 1978, Hunter 1985, Cailliet et al. 1986). It is recommended by Hunter et al. (1985) as the only preservative appropriate for use with the hydrated oocyte method. This is because the hydrated oocyte method estimates batch fecundity by calculating the number of hydrated, unovulated oocytes in gravid ovaries, and Gilson's destroys hydrated oocytes (Hunter et al. 1985).

Formalin preservation has the advantages over Gilson's of (1) preserving hydrated as well as other oocytes over long periods of time, (2) having a short fixation period and (3) low shrinkage rates, varying from 0 to 7% (Hiemstra 1962, Fleming & Ng 1987, Hislop & Bell 1987), and (4) relative ease of handling (Hunter et al. 1985, Cailliet et al. 1986, Schaefer 1987, West 1990). Its greatest disadvantage is that oocytes and ovarian tissue may become fixed into a hard mass, making it extremely difficult and tedious to separate oocytes without damage (Schaefer & Orange 1956, Bagenal & Braum 1978, Cailliet et al. 1986).

In this paper we propose a new, two-step method to obtain hardened, separated oocytes for fish reproduction studies. Oocytes are physically separated before being preserved in formalin, thus maintaining the advantages of formalin fixation and preservation while also providing well-separated oocyte samples. The objectives of this paper are to (1) describe this new method and evaluate its effectiveness, (2) determine the shrinkage rates of weakfish *Cynoscion regalis* oocytes separated and preserved by this method, after 3–4 and 6–7 mo preservation, and (3) assess the appropriateness of this method for use with the hydrated oocyte method of estimating batch fecundity (Hunter et al. 1985).

Methods

Twenty-eight weakfish *Cynoscion regalis*, with ovaries in the hydrated but unovulated developmental stage, were collected in the summer of 1991. Fresh (unpreserved) oocytes were removed from the right ovary of each fish and spread onto a microscope slide. Twenty hydrated oocyte diameters were then measured, after a minimum sample size of 15 oocytes was determined using the iterative method described in Sokal & Rohlf (1981) ($S=0.05$, $\alpha=0.05$; $P=0.90$, $\delta=0.06$ mm). An ocular micrometer in a dissecting microscope was used to measure oocyte diameters to the nearest 0.038 mm (1 micrometer unit at a total magnification of 24×). Measurements were taken along the median axis of the oocyte, parallel to the horizontal micrometer gradations (Macer 1974, DeMartini & Fountain 1981).

Ten of these fish were also used to estimate batch fecundities gravi-

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metrically (Bagenal & Braum 1978), using the hydrated oocyte method (Hunter et al. 1985). A 0.2 g subsample of fresh oocytes was taken from the middle of the right ovary, and all hydrated oocytes in each subsample were counted under a dissecting microscope at a magnification of 24×.

Oocytes were separated from one another and the ovarian membrane through a washing process. Each ovary was slit longitudinally, turned inside out, and held under vigorously flowing tapwater. This flushed the oocytes out of the ovarian membrane and into a 0.01 mm mesh sieve, which was held beneath the ovary. Oocytes collected in the sieve were again rinsed with fully-flowing tapwater to help separate them from one another. The whole procedure took 5–10 min per ovary.

After draining the water, oocytes were transferred to containers where they were preserved in 2% neutrally-buffered formalin. This formalin concentration was chosen because it was the lowest possible concentration that would ensure proper oocyte preservation while minimizing changes in oocyte size and appearance.

The equipment necessary for the washing process is very basic. We used two standard faucets (2 cm diameter), with flow rates of 133 and 286 mL/s, respectively. Both faucets had sufficient hydraulic pressure to dislodge oocytes of all stages from ovarian tissue. However, the faucet with the higher flow rate, and thus greater water pressure, worked best. Any sieve with mesh small enough to retain less-developed oocytes, and deep enough to keep them from being flushed over the edge during washing, can be used as a collecting sieve. We used a sieve made from a piece of nylon plankton net (0.01 mm mesh) inserted between two sections of 10 cm diameter PVC pipe, with a depth (from lip to the mesh layer) also of 10 cm (Fig. 1).

Preserved oocytes were measured 3–4 mo after collection and, again, 6–7 mo after collection. Samples were stirred before oocytes were removed to reduce bias due to settling differences caused by oocyte size or density. Oocytes were then dipped out of the formalin with a spoon and placed in a gridded petri dish. The first 20 undamaged hydrated oocytes were measured along the median axis as described for fresh oocytes. Oocyte damage, due to the washing process, was evaluated by assessing the percentage of damaged oocytes in subsamples of 50 hydrated oocytes from each of 10 preserved samples. We considered as damaged those oocytes which were partially collapsed and thus not appropriate for diameter measurements.

Batch fecundities were also estimated gravimetrically from preserved samples (after 3–4 and 6–7 mo preservation) using oocyte samples from the same 10 fish originally used to estimate batch fecundities from fresh samples. Oocytes were stirred, decanted into a sieve, drained of formalin, and washed with tapwater. Oocytes were removed from the sieve, spread on the bottom of a petri dish, and blotted dry with tissue paper. A 0.2 g subsample was then transferred to a gridded petri dish. A small amount of tapwater was added to keep the oocytes moist and to help distribute them evenly over the bottom of the dish.

One-way analysis of variance (ANOVA) was used to evaluate differences between fresh and preserved oocyte diameters and batch fecundity estimates. Individual females were used as blocks to remove the effect of variation among females. To compare batch fecundities based on fresh samples with those based on preserved samples, it was important to evaluate the within-ovary positional effect. This was necessary because fresh oocyte samples were taken from the middle of the ovary, whereas preserved samples came from mixed areas (due to the washing process). Hydrated oocytes were counted in 0.2 g oocyte samples taken from the anterior, middle, and posterior areas of 28 fresh ovaries.

Mean oocyte shrinkage was calculated for each of the 28 ovaries after 3–4 and 6–7 mo preservation. Mean oocyte shrinkage was then plotted against mean fresh hydrated oocyte diameter to evaluate whether oocyte shrinkage was consistent over the size-range of hydrated oocytes.

All data were analyzed using statistical methods available through the Statistical Analysis System (SAS 1988). Model assumptions were evaluated by examination of residuals (Draper & Smith 1981). Batch fecundity data was $\log_{10}$-transformed to meet the assumption of homogeneity of variances.

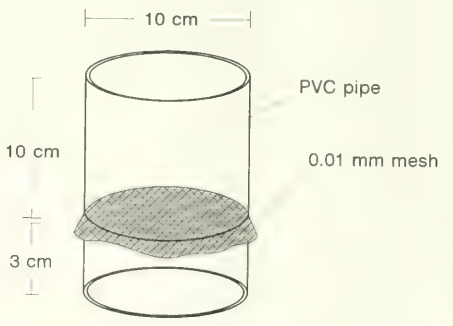

Figure 1

Schematic representation of the sieve used to collect weakfish *Cynoscion regalis* oocytes dislodged during the washing process.

Results

We successfully used this separation technique on ovaries in all stages of development and observed little or no damage to the oocytes (Figs. 2, 3). The percentage of damaged oocytes ranged from 0 to 6%, with an average of 2%. None of these, however, were structurally damaged, i.e., no empty chorions were found. Because such low percentages of slightly-degenerated hydrated oocytes can also be found in fresh oocyte samples—i.e., some hydrated oocytes are never ovulated and will be resorbed, and some ovulated oocytes are never spawned (e.g., Clark 1934, DeMartini & Fountain 1981)—we considered oocyte damage due to the washing process to be negligible.

Oocytes in all stages (primary growth to hydrated) were obtained in sufficiently large numbers and correct proportions to develop oocyte size-frequency distributions (Fig. 2). For most ovaries it was possible to flush virtually all oocytes out of the ovarian membrane. However, we found it was easier to dislodge oocytes in well-developed ovaries than in early-developing or resorbing-phase ovaries.

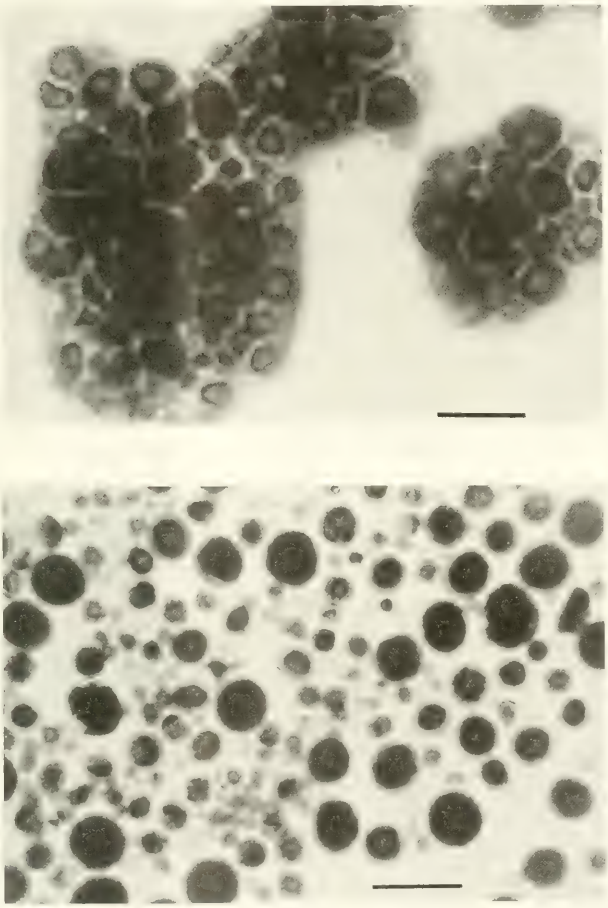

Figure 2
Appearance of weakfish *Cynoscion regalis* oocytes in various developmental stages: **(top)** fresh and **(bottom)** after hydraulic separation and fixation in 2% formalin. Bars=1 mm.

Formalin (2%) successfully fixed and then preserved weakfish oocytes for over 6 months with minimal effect on their appearance and size. There was no need for a separate, higher-concentration fixative. Atretic and hydrated oocytes were more opaque after preservation, but much less so than when kept at higher formalin concentrations. After 6 months, hydrated oocytes were still easily recognized by their larger size and greater translucence than were less-developed oocytes (Fig. 3). Most oocytes, in all stages, retained their spherical shape.

Hydrated oocytes had a highly significant decrease in diameter after preservation, with a range of 0–11% shrinkage after 3–4 mo in preservative (F=223.25, N=560, P<0.01). The average oocyte shrinkage, however, was only 5% and after more than 6 months, oocyte shrinkage had not significantly increased (F=1.91, N=560, P=0.17). Mean shrinkage of hydrated oocytes preserved for 3–4 and 6–7 mo showed no relationship with their original mean fresh diameters (Fig. 4), indicating that an oocyte's stage in the hydration process did not affect its rate of shrinkage.

Batch fecundities estimated from fresh oocyte samples were

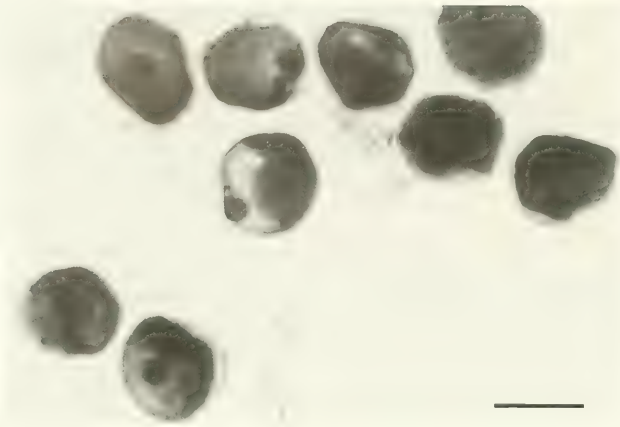

Figure 3
Appearance of weakfish *Cynoscion regalis* hydrated oocytes after 6–7 mo preservation in 2% formalin. Bar=1 mm.

not significantly different (F=0.0027, N=10, P=0.14) from those estimated from samples preserved for both 3–4 and 6–7 mo (Table 1). Batch fecundities estimated from fresh and preserved samples could be compared because no positional effects were found between counts from different areas (ANOVA, F=0.91, N=28, P=0.41).

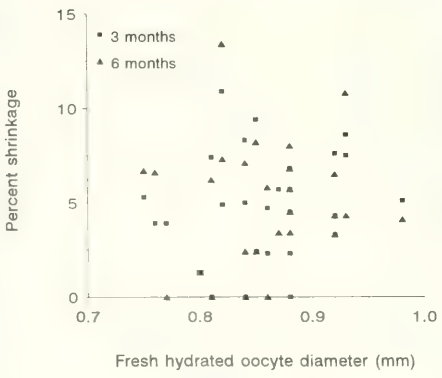

Figure 4
Mean shrinkage of hydrated oocytes of weakfish *Cynoscion regalis* after 3–4 and 6–7 mo preservation in 2% formalin.

Discussion

There is need for a reliable method of separating and preserving fish oocytes. Generally, separated and preserved oocytes are used to estimate oocyte size and develop oocyte size-frequency distributions, as well as in the hydrated oocyte method of determining batch fecundity. Researchers often want to evaluate changes in egg size over the spawning season, or between spawning seasons (e.g., DeMartini 1990), and oocyte size-frequencies are used to assess whether fish have determinate or indeterminate fecundity (Hunter & Macewicz 1985). The hydrated oocyte method appears to be the easiest and most accurate way to determine batch size in serial spawners (Hunter et al. 1985). All of these types of analyses are integral to reproductive studies of multiple-spawning fishes, and yet their accuracy depends on using either fresh oocyte samples or oocyte samples separated and preserved in a reliable fashion.

Although still widely used, researchers are beginning to recognize a number of problems with the use of Gilson's solution as a preservative. It degenerates hydrated oocytes (Hunter et al. 1985, Schaefer 1987, Brown-Peterson et al. 1988), making it impossible to use the hydrated oocyte method to estimate batch fecundity (Hunter et al. 1985). It causes a high rate of

Table 1
Batch fecundities of weakfish *Cynoscion regalis* estimated from fresh oocyte samples and from oocyte samples preserved for 3–4 and 6–7 mo in 2% formalin.

Fish#	Fresh count	After 3 mo preservation	After 6 mo preservation
1	159,400	140,400	154,700
2	101,700	104,800	95,700
3	190,000	212,700	208,300
4	158,900	176,300	156,800
5	171,100	174,000	181,400
6	155,100	149,000	143,300
7	208,400	167,800	223,100
8	161,000	154,200	191,800
9	144,700	127,200	148,300
10	209,000	172,200	216,100

oocyte shrinkage (DeMartini Fountain 1981, Schaefer 1987, Witthames & Greer Walker 1987), which could mask gaps found naturally in oocyte size-frequency distributions. Gilson's solution also causes continuous shrinkage over time (Witthames & Greer Walker 1987), which could make any comparisons of egg diameter during the spawning season, or between consecutive years, meaningless unless all samples were preserved for the same amount of time.

Formalin at low concentrations (3–5%) meets the requirements of both an oocyte fixative and preservative (Markle 1984). It prevents microbial activity, with minimal effect on shape, cell contents, and osmolarity. As a preservative, it maintains this state, is relatively mild, stable, and long-lasting (Snyder 1983, Markle 1984). Although formalin is commonly used to preserve ichthyoplankton samples (Snyder 1983), it has not been commonly used for adult fish-reproduction studies. This is due to the tendency for formalin to fix the whole ovary into a hard mass, from which it is difficult to separate individual oocytes (Schaefer & Orange 1956, Bagenal & Braum 1978).

By physically separating the oocytes before preservation in formalin, our method overcomes the problem of oocyte separation while maintaining the advantages of using formalin as a preservative. This method is inexpensive, quick, and much less toxic than Gilson's, providing researchers with undamaged oocytes of all stages, with little effect on appearance or size. This new method has been successfully used on weakfish and two other sciaenids (Atlantic croaker *Micropogonias undulatus*, and black drum *Pogonias cromis*; unpubl. data), and, given the similarity of teleost ovaries, should be applicable to a wide range of species. Additionally, because oocytes are preserved in a low concentration of formalin, similar to the preservation of most plankton samples, hydrated oocytes processed in this fashion would be comparable to those collected and preserved during plankton studies. This would make it possible to better link adult fish-reproduction studies with those from egg surveys.

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Vertical and horizontal movements of adult chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary

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Maturing salmon leave oceanic feeding grounds and migrate towards their natal rivers, converging on coastal and estuarine waters. Although the passage through an estuary represents a physical and physiological milestone during the homing migration of salmon and is often a period of heavy commercial and sport harvest, relatively little is known about how oceanographic processes might affect the distribution of salmon. Estuaries are transition zones between coastal and riverine waters, and are areas of rapidly changing temperature, salinity, and current regimes which may present migrating fish with osmo- and thermoregulatory challenges. Furthermore, estuaries may also represent a transition zone for the orientation mechanisms salmon use to find their natal stream (McKeown 1984).

Several investigators have observed the horizontal movements of Atlantic salmon *Salmo salar* (Stasko 1975), sockeye salmon *Oncorhynchus nerka* (Groot et al. 1975), and chinook salmon *O. tshawytscha* (Fujioka 1970) in estuaries, and observed both passive and active movements with and into tidal currents. More recent tracking studies of maturing Atlantic salmon, sockeye salmon, chum salmon *O. keta*, and steelhead trout *O. mykiss* in coastal waters have demonstrated that their vertical movements may be related to the local vertical stratification of the water column (Westerberg 1982, Soeda et al. 1987, Quinn et al. 1989, Ruggerone et al. 1990). No studies are presently available which describe both the vertical and horizontal movements of salmon within an estuary.

The following study was designed to describe the short-term movements of adult chinook salmon in the Columbia River estuary outfitted with pressure-sensitive ultrasonic tags to (1) relate these movements to tidal currents and the temperature and salinity structure of the water column, and (2) examine how these movements might be explained by their physiology and the need for orientating clues.

Materials and methods

Study site description

The Columbia River has a large estuary with tidal influence extending approximately 161 km upriver from the mouth, although salt intrusion extends no more than 48 km upriver along the bottom (Simenstad et al. 1984). Average monthly river flows from 1969 to 1982 were 7460 m^3/s with a range of 4070 m^3/s in September to 10,530 m^3/s in June (Simenstad et al. 1984). This estuary has mixed semidiurnal tides; that is, each tidal day has two high and two low tides of unequal size (Jay 1984). The mean tidal range (mean high water to mean low water) measured over 138 tides in 1958 was 2.31 m at North Jetty (Fig. 1; Jay 1984).

Ultrasonic telemetry

Chinook salmon were captured during the morning of each tracking day with short (~5 min) drifts using 90–180 m of 21 cm stretched-mesh commercial gillnet (~12 m in depth) which fished the entire water column. When a fish was detected, the net was immediately retrieved, and the fish removed and placed in a 100 L cooler filled with surface water. If more than one chinook was captured, one was selected for tracking based on scale retention, lack of scars, and general activity level. Total length was measured to the nearest cm, and a numbered disc tag was attached below the dorsal fin. A pressure-sensitive (74 mm long × 16 mm in diameter) ultrasonic transmitter (Vemco Ltd.), weighing 13 g in water and calibrated within ±1 m to a conductivity/temperature/depth probe (CTD; InterOcean model 513) prior to the track, was inserted into the stomach of the unanesthetized fish. The fish was placed in the boat's partially-filled watertight fish locker (2.5×1.5×0.5 m) for recovery (~30–45 min). The holding tank allowed the fish to reach the surface, gulp air, and inflate its swimbladder. All fish were captured in

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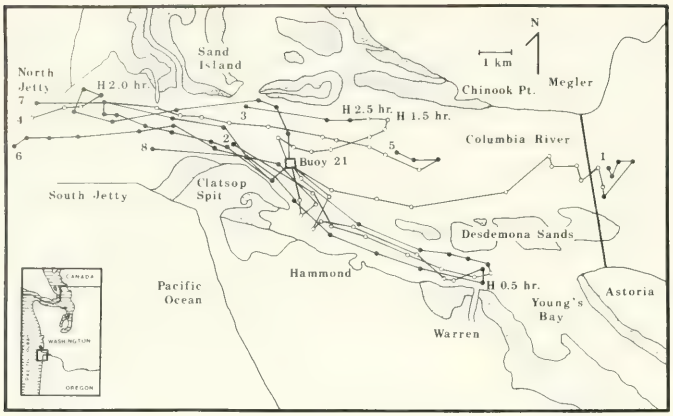

Figure 1
Study area and track maps of horizontal movements by chinook salmon *Oncorhynchus tshawytscha* tracked in the Columbia River estuary. Sampling during flooding ( ) and ebbing (●) tides. Each circle represents 30 min of tracking time. 'H' indicates extended holding period occurred.

relatively shallow water (about 5 m) on the south side of Sand Island (except Fish 1 which was captured on the north side of Desdemona Sands), and all fish were released at Buoy 21 (Fig. 1).

A single fish was released each day and followed primarily during daylight hours from the gillnet vessel *Midnight Gambler*. Transmitted signals were received by a directional hydrophone and tunable receiver/decoder (Vemco Ltd.). During tracking, the boat typically stayed 50–400 m away from the fish, and the following data were collected: (1) boat position every 5 min from a loran C receiver; (2) water depth beneath the boat every 5 min from a fathometer; (3) fish depth every 1 min from the decoder; (4) approximately every 30 min the fish was more closely approached (usually to within 50 m, based on triangulation and signal strength), and secchi disk and CTD casts were made while the boat drifted. CTD casts took about 5 min to perform and measured the conductivity and temperature at intervals of 1 or 2 m, usually to within 4 m of the bottom. In deeper waters, casts were generally limited to 12 m to avoid losing the fish. Except for fish swimming close to the bottom, this range always encompassed the depth at which the fish was swimming and any large changes in temperature or salinity.

Data analysis

Boat positions were used to reconstruct each fish's path on a horizontal track map and to determine ground speed. A 15 min sampling interval was chosen to calculate ground speeds because shorter intervals may overestimate fish speed due to extraneous boat movements, and longer intervals may underestimate fish speed because calculations based on a straight line between positions may mask shorter-scale movements. Water and fish depths were used to reconstruct each fish's path on a vertical track map. Conductivity was converted to salinity (Perkin & Walker 1972) for construction of temperature and salinity profiles.

To determine whether salmon showed preferences for ranges of temperature or salinity, the salinity and temperature of the water experienced by each fish were determined indirectly by substituting the appropriate values from the temperature and salinity profile for the depth at which the fish was swimming during each observation. Salinities and temperatures between the measured depth-intervals were determined by linear interpolation. The range of temperatures and salinities available to each fish was determined from temperature and salinity profiles separated into 1-unit (°C or ‰) intervals. The fraction of the water column that each unit of temperature or salinity occupied within the sampled depth was calculated and multiplied by the time-interval of the representative temperature and salinity profile. Each temperature and salinity profile was assumed to represent water conditions over a time-interval midway between consecutive profiles. Fish that swam near the bottom sometimes exceeded the depth of the CTD casts, and these observations were omitted from analysis of salinity or temperature preference. Frequencies of temperature and salinity were summed over all profiles for each track to obtain the salinity and temperature distribution available to each fish. These distributions were tested statistically by goodness-of-fit analysis to determine if the distributions of available and experienced conditions were similar. Differences were assumed to indicate fish were displaying non-random vertical movements, presumably to select for a favorable combination of environmental factors.

Results

Eight chinook salmon were tracked in the Columbia River estuary from 27 August to 5 September 1987, resulting in 56:39 h of tracking time over more than 127 km (Table 1). Mean river flow over Bonneville Dam during the study period was 2910 m^3/s (range 2370–3430 m^3/s; Fish Passage Center, Corvallis OR). Secchi disc measurements taken intermittently during all tracks had a pooled average depth of 2.47 m (range 1.43–4.12 m for individual tracks). In general, signal reception in the estuary was good and no fish were lost during the tracking period. Tracking of a fish was terminated owing to danger of vessel stranding on mudflats (Fish 1), high waves at the river entrance sandbar (Fish 2,4,8), darkness (Fish 3), or fish movement into the ocean (Fish 6,7). Only Fish 5 was followed during periods of darkness (1:09 h). Five of the eight fish (Fish 2,5,6,7,8) had dark or dusky skin color, indicative of lower-river stocks known as tules. Bright-skinned fish (Fish 1,3,4) may have derived from either tules or upriver brights. All upriver brights enter the river with a more "oceanic" appearance and return to spawning grounds and hatcheries primarily near the Hanford Reach (Howell et al. 1984); however, some tules also enter the river in bright ocean-type condition.

Horizontal movements

Fish usually moved in the direction of the prevailing tidal current, and reversals in direction and a milling/holding behavior were often associated with changing tides (Fig. 1). The average ground speed (weighted by the number of sampling intervals) for tracked fish was 2.33 km/h (range 1.28–3.17 km/h for individual fish (Table 1). Ground speeds are the resultant of two vectors: velocities (speed and direction) of the tidal current and of the tracked fish. When analyzed by tidal stage, mean ground speeds for individual fish ranged from 0.74 to 4.08 km/h (2.60 overall) during ebbing tides, and 0.91 to 3.12 (2.04 overall) during flood tides (Table 2).

Two chinook salmon were recovered after the tracking period. Fish 2 was recaptured 14 d after release during test fishing operations 93 km from the river mouth, and Fish 7 was recaptured 9 d after release by a sportsman about 80 km from the river mouth. These fish had net travel rates of 6.0 and 7.8 km/d, respectively, after release.

Vertical movements

Mean fish depth was 5.5 m, and mean water depth beneath the boat was 13.4 m (Table 3). Vertical profiles of temperature and salinity indicated extremely dynamic hydrographic regimes. Within a single track, some profiles indicated nearly uniform temperatures and salinities over all depths, while others revealed strong haloclines and thermoclines. Vertical track maps (Fig. 2), and fish-depth frequency distributions relative to mean temperature and salinity profiles (Fig. 3) for Fish 4 and 5, show two observed patterns of vertical movement: Some salmon swam in brackish surface waters with large vertical gradients of salinity and temperature and made occasional excursions into uniform bottom waters (Fish 2,6,7,8), whereas others demonstrated periods of swimming in the water column and near the bottom (Fish 1,3,4,5). Some vertical track maps show fish that appear to be deeper than

Table 1

Summary statistics for tracks of adult chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary. Gross distances traveled and average speeds were based on 15 min sampling periods.

Fish	Release date	Release time	Fish total length (cm)	Time tracked (h:min)	Gross distance traveled (km)	Mean ground speed (km/h)	Reason for ending track
1	Aug. 27	11:12	91	7:18	11.73	1.89	Possible vessel stranding
2	Aug. 28	12:53	84	6:29	18.52	2.96	High waves at river entrance
3	Aug. 29	12:19	86	7:44	9.75	1.28	Darkness
4	Sept. 1	10:55	76	7:20	16.16	2.23	High waves at river entrance
5	Sept. 2	10:12	96	10:52	24.41	2.26	Darkness
6	Sept. 3	10:44	83	4:26	12.29	2.89	Movement into ocean
7	Sept. 4	09:57	76	4:33	14.27	3.17	Movement into ocean
8	Sept. 5	09:40	81	7:57	20.56	2.65	High waves at river entrance
Mean			84	7:05	15.96	2.33	
Total				56:39	127.69		

Table 2

Mean ground speeds and sample sizes during ebb and flood tides based on 15 min sampling intervals for chinook salmon *Oncorhynchus tshawytscha* tracked in the Columbia River estuary.

	Ebb		Flood	
Fish	Ground speed	Sample size	Ground speed	Sample size
1	0.74	15	3.12	14
2	4.08	9	2.34	16
3	1.86	12	0.19	19
4	2.98	17	1.17	12
5	1.71	5	2.54	21
5	2.09	17		
6	3.01	15	2.01	2
7	4.09	11	1.73	7
8	3.10	15	2.24	16
Pooled	2.60	116	2.04	107

the bottom. This resulted from recording water depth under the boat, which generally followed a short distance behind the fish rather than directly above it. Although this discrepancy makes it impossible to accurately determine the distance of the fish from the bottom, Fish 1 and Fish 3 spent the majority of their time close to or on the bottom, and Fish 4 spent approximately 35% of its time near the bottom.

Fish encountered a wide range of salinities (7.8–33.6‰) and temperatures (8.9–22.9°C; Table 3). Due to the dynamics of tidal currents and vertical water structure within the estuary, the frequency distributions of available salinities and temperatures were different for all fish tracks (log-likelihood test, Zar 1984; $p<0.001$). Hence, it was impossible to compare the distributions of temperature and salinity experienced by individual fish. No analysis was made on the depth data transformed to salinity and temperature for portions of fish tracks below depths sampled by the CTD, because the available frequency distributions of salinity and temperature could not be calculated for these depths and the distance from the fish to the bottom could not be accurately determined. Due to these problems, an average of 83.2% (range 50.9–100%) of the depth observations for individual tracks were converted to experienced salinity and temperature. Fish 3 was not analyzed for temperature and salinity preference because it spent nearly all its time below depths sampled with the CTD. However, the frequency distributions of temperatures and salinities occupied by fish showed modes between 14° and 16°C for five of seven fish, and 17 and 19‰ for four of seven fish (e.g., Fish 4 and 5, Fig. 4). The log-likelihood test indicated that all fish occupied different distributions of temperature and salinity than they would have experienced by random vertical movements in their environments ($p<0.001$).

Discussion

In general, the tracked fish moved with tidal currents, milled during periods of low current velocity, and reversed their direction of movement with the change of tides. The results suggest that tidal currents are a major component to horizontal fish movements in the Columbia River estuary. Chinook salmon had higher mean ground speeds during ebbing tides than during flooding tides, presumably because tidal and riverine flows are additive during ebbing tides and antagonistic during flooding tides.

These findings tend to agree with other estuarine tracking studies (Groot et al. 1975, Fujioka 1970) of Pacific salmon. Fujioka (1970) found that the position of chinook salmon tracked in the Duwamish River estuary was dependent on the tidal stage, with fish generally

Table 3

Mean, maximum, and sample size of fish-depth observations; mean, minimum, and maximum water depth beneath the tracking boat; and fish-depth observations transformed to salinity and temperature experienced by tracked chinook salmon *Oncorhynchus tshawytscha* within the Columbia River estuary. CTD = conductivity/temperature/depth probe.

	Fish depth (m)			Water depth (m)				Salinity (‰)			Temperature (°C)			
Fish	Mean (SD)	Max.	*N*	Mean (SD)	Min.	Max.	*N*	Mean (SD)	Min.	Max.	Mean (SD)	Min.	Max.	Max. CTD depth (m)
1	4.6 (1.9)	10.2	406	5.8 (2.7)	1.2	12.5	89	12.9 (3.6)	7.8	19.8	17.0 (2.0)	13.0	22.9	12
2	2.0 (1.0)	8.1	374	12.1 (2.9)	6.7	18.3	78	16.0 (3.4)	8.0	27.4	16.8 (1.9)	11.8	20.0	12
3	17.1 (5.7)	24.9	440	16.5 (3.6)	7.9	23.8	92							10
4	7.9 (5.6)	22.3	405	14.6 (4.9)	3.7	29.3	89	18.4 (5.5)	9.1	32.7	15.0 (2.1)	8.9	18.1	12
5	2.1 (1.6)	24.2	618	14.2 (7.3)	4.3	30.5	129	20.4 (3.8)	13.0	32.6	14.4 (1.3)	9.4	16.8	14
6	2.3 (1.7)	9.5	249	16.2 (5.6)	7.9	29.3	51	25.5 (3.4)	16.8	32.3	13.6 (1.5)	10.5	16.0	12
7	3.3 (3.6)	16.1	235	15.4 (6.4)	7.0	30.2	55	25.3 (5.2)	17.4	33.6	13.0 (1.8)	8.9	15.5	10
8	2.8 (1.2)	10.8	437	13.7 (2.9)	6.7	19.8	92	18.7 (2.3)	10.6	31.3	15.6 (1.1)	10.0	19.1	12
Pooled	5.5 (3.3)	24.9	2675	13.4 (4.9)	1.2	30.5	675	19.4 (3.8)	7.8	33.6	15.1 (1.6)	8.9	22.9	

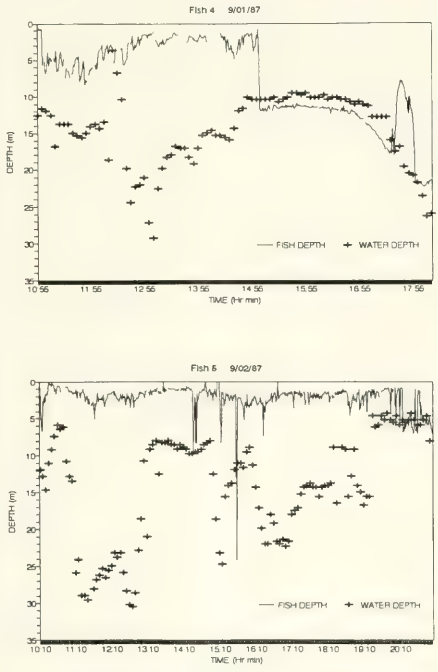

Figure 2
Track maps of vertical movements by Fish 4 and 5 within the Columbia River estuary.

further upstream during a high tide compared with a preceding or subsequent low tide. Similarly, Groot et al. (1975) found that sockeye salmon tracked in the Skeena River estuary tended to drift with the current. They also observed that during ebb tides, some fish exited the estuary and relatively few fish made any net movement upriver. Average ground speeds were slightly higher for Columbia River chinook (2.41 km/h) than the Skeena River sockeye (1.81 km/h in 1969 and 2.25 km/h in 1970), but these differences may merely reflect the tidal current regimes of the two estuaries.

Previous tagging studies have demonstrated that delays in estuaries of about one month are common in Pacific salmon (Wendler 1959, Verhoeven & Davidoff 1962, Vernon et al. 1964). Based on the period when marked fall chinook salmon are captured in the Columbia River commercial gillnet fishery, lower river tules delay in the estuary but upriver brights pass through relatively rapidly (Donald O. McIssac, Oreg. Dep. Fish Wildl., Portland, pers commun.). The movement of tracked fish with tidal currents and the lack of substantial net upriver progress support the hypothesis that fall chinook may spend an indeterminate amount of time holding within the estuary prior to upstream movements.

Tracked chinook displayed two vertical movement patterns: swimming close to the bottom, or a combination of swimming in midwater and close to the bottom. Time spent near the bottom may have been an alternative stock-specific behavioral pattern for tracked fish, or may have been influenced by stress from the capture and tagging procedure. Sockeye salmon tracked in deeper waters and for longer periods than the present study demonstrated characteristic vertical and horizontal movements about 1 h after release (Quinn et al. 1989). Stressed fish would be expected to show lethargic vertical and horizontal movements, and, as such, fish in the present study were considered to be behaving normally because all fish demonstrated substantial vertical movements during portions of their tracks.

The vertical distribution of salmon in estuaries may be in-

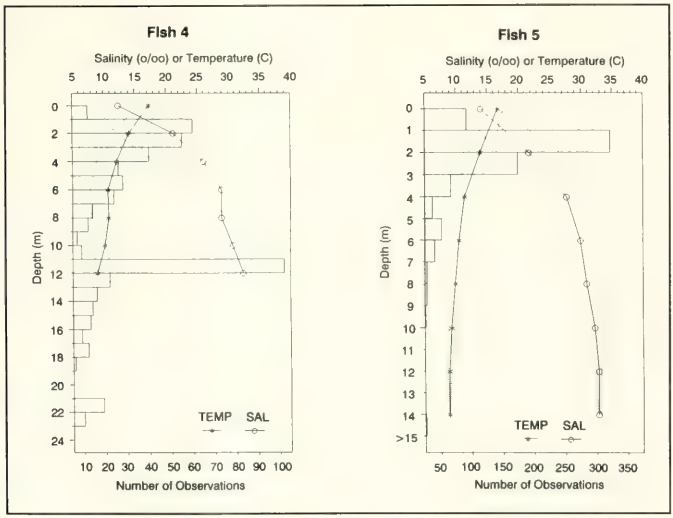

Figure 3
Mean temperature and salinity depth profiles and depth distributions for tracks of Fish 4 and 5. Dotted lines indicate 1SD.

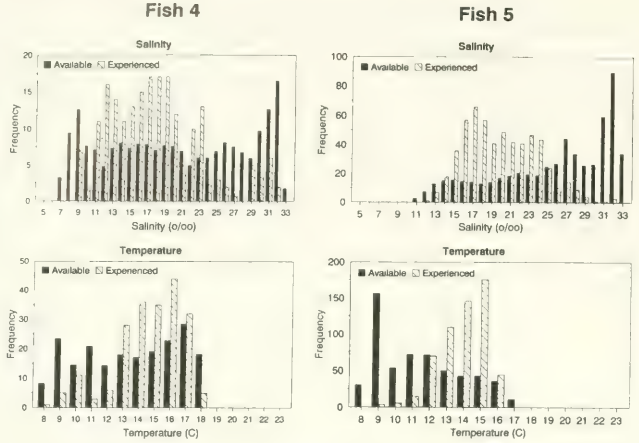

Figure 4

Histograms of experienced and available temperature and salinity distributions for Fish 4 and 5.

fluenced by species- or stock-specific preferences for particular temperature or salinity regimes, light levels, positions in the water column (relative to the surface or bottom), or by the need to locate orientating clues. Our observations of tracked chinook making vertical movements through large ranges of salinity and temperature indicate that they are tolerant of rapid, short-term changes in these features over several minutes, but utilized intermediate salinities and intermediate-to-warm temperatures while swimming in midwater. The presence of a lag time in equilibrating internal and external ion concentrations and temperatures could explain their ability to tolerate rapid changes in these factors because adult chinook salmon have been observed to require 30–60 min to equilibrate their internal temperature to ambient water temperature when moved between 19° and 9°C, depending on direction of the transfer and size of the fish (Berman & Quinn 1991).

Vertical movements which determine long-term internal temperature may be affected by energetic factors related to stock origin. Stocks such as upriver brights which have extensive in-river homing migrations might be expected to take advantage of the cooler water near the bottom of the estuary. Brett & Glass (1973) reported that oxygen consumption for a 5 kg sockeye salmon would be about 20–40% less in 10° than 20°C water, depending on whether the fish was at rest or active. Assuming a similar relationship for chinook salmon, most fish characterized as tules in the present study were not minimizing their energy-expenditure rate while swimming in midwater, as they did not prefer the coolest water. Indeed, several often occupied relatively warm water (Fig. 5, Table 3). In contrast to the dark- and dusky-skinned fish which swam primarily in midwater, the three bright fish (Fish 1,3,4) potentially from upriver stocks swam for substantial periods near the bottom and may have been attempting to minimize their energy expenditures by utilizing the coolest waters available to them in the water column.

In contrast, a fish's preferred mean external salinity may be affected by its current physiological status and the degree to which the osmoregulatory system has switched its direction of active ion transport. Vertical salinity and temperature gradients are often correlated in estuarine environments, and the maturity level of a tracked fish is unknown; therefore, determining the degree to which salinity or temperature affect vertical movements is confounded in field experiments.

Fish orienting to olfactory stimuli (Hasler & Scholz 1983) might be expected to move up and down through the halocline (Westerberg 1982, 1984), and fish tracked in the Columbia River estuary were observed at depths containing large vertical gradients of salinity and temperature. Olfaction is an important component in homing by salmonids in rivers and streams (Hasler & Scholz 1983), but it is unclear to what extent and how olfaction is utilized for orientation in coastal and estuarine waters. Westerberg (1984) hypothesized that salmonids might derive information from the current shear at haloclines separating water layers containing different concentrations of natal river olfactants. Tracking data on Atlantic salmon *Salmo salar* by Westerberg (1982) and Doving et al. (1985) supported this hypothesis, demonstrating characteristic and regular dives to the halocline one or two times per hour. Data for Pacific salmon and steelhead trout in coastal waters (Ichihara & Nakamura 1982, Quinn & terHart 1987, Soeda et al. 1987, Quinn et al. 1989, Ruggerone et al. 1990) show a less clear pattern of vertical movements relative to the thermocline than that reported by Westerberg (1982) and Doving et al. (1985). Results of sockeye tracking (Quinn & terHart 1987, Quinn et al. 1989) in both mixed and stratified waters demonstrated

that fish were generally surface-oriented in mixed waters and remained at or below the thermocline in stratified waters. In contrast, steelhead trout spent up to 96% of their tracked time within 1m of the surface, but made occasional dives through the thermocline/halocline located 5–7 m below the surface (Ruggerone et al. 1990). Ichihara & Nakamura (1982) reported that chum salmon *O. keta* in coastal waters off Japan spent 44% of their time within 5 m of the surface, and seldom dove through the thermocline. On the other hand, Soeda et al. (1987) reported that a chum salmon tracked for 57 h off the north Hokkaido coast spent much of its time swimming within the thermocline.

The vertical salinity and temperature profiles in this study showed that water structure ranged from uniform to highly stratified during a single tracking period. Chinook spent most of the tracked time either close to the bottom or within the salinity gradient, i.e., within the water layers predicted by Westerberg's (1984) hypothesis. Tracking studies of Atlantic and Pacific salmon suggest that the vertical movements of salmonids may be influenced by haloclines or thermoclines, but do not always demonstrate a consistent pattern of vertical movements relative to the water structure. These differences suggest that salmonids may have multiple mechanisms for orienting during their homing migrations which may change according to level of maturity, proximity to the home river, and the vertical water structure.

Moreover, if salmon derive directional information from current shears at the halocline, they may be able to maintain directed swimming using other guidance mechanisms (e.g., sun or magnetic compass). If so, only occasional excursions through the halocline may be sufficient for orientation, and other factors may affect their position in the water column. Thus, variation in vertical movement patterns among species and study sites does not contradict Westerberg's (1984) hypothesis.

In summary, tracked chinook salmon demonstrated no substantial net upstream movements while under observation, and tidal currents were a major factor influencing their horizontal movements. Two patterns of vertical movements were observed: Fish tended to swim in surface waters where salinity and temperature gradients were greatest, or they swam near the bottom. Vertical movements may have been influenced by temperature and salinity preferences related to stock origin and individual physiological requirements, or movements may have been used as a searching strategy for clues to orientation. Despite the lack of net upstream horizontal movements, the vertical movements of tracked chinook tended to support predictions that the vertical distribution of homing salmonids are influenced by water column structure which may be utilized for orientation towards natal river systems (Westerberg 1984).

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Occurrence of *Echeneibothrium* (Platyhelminthes, Cestoda) in the calico scallop *Argopecten* gibbus from North Carolina

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Scallops are known hosts for larval parasites (Cheng 1967). Nematode and trematode parasites have been described in the calico scallop *Argopecten gibbus*, a bivalve native to the Atlantic coast (Cummins et al. 1981). Larval cestodes of the genera *Parachristianella*, *Tylocephalum*, *Rhinebothrium*, and *Polycephala* have also been described in *Argopecten irradians* populations from the Gulf of Mexico (Cake 1977).

During the course of a study describing gametogenesis and reproductive periodicity in the North Carolina population of *A. gibbus*, a larval cestode was found in specimens collected in late 1990 and early 1991. The objectives of this report are to identify the cestode, and to describe alterations in intestinal morphology and percent dry weight of the gonadal tissues ("gonadal index") of *A. gibbus*, which coincided with infection by this cestode.

Materials and methods

Calico scallops were collected by personnel of the North Carolina Division of Marine Fisheries or by commercial fishermen at 1–3 mo intervals from January 1990 to February 1991. Collection sites were located 10–20 km offshore (33–35° lat., 76–77° long.) from Cape Lookout, North Carolina at depths of 30–40 m. The scallops were placed on ice, transported to the lab, and the tissue processed within 24 h.

Gonads were removed and fixed in a seawater Bouin's solution for 12–24 h. After dehydration in a graded ethanol series, the gonads were embedded in paraffin and sectioned at 7 µm. Tissues were stained with either hematoxylin and eosin Y or Mallory's trichrome stain (Humason 1962).

Dry weights of tissues were determined by separating gonads, adductor muscle, and the remaining tissues, and drying each tissue to constant weight in an oven at 60°C (~48 h). Dry weight of the gonad was expressed as a percentage of the total dry weight to obtain the gonadal index. An analysis of variance (ANOVA) was used to test for differences in the gonadal indices of scallops from parasitized and nonparasitized groups in the same stages of gametogenesis.

Results

Encysted parasites, identified by Dr. Thomas C. Cheng (Medical Univ. South Carolina, Charleston) as the plerocercoid stage of the cestode *Echeneibothrium* sp., were found within the connective tissue of the gonads in calico scallops collected only during November 1990 and February 1991 (Fig. 1). Levels of

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Figure 1
Longitudinal section of *Echeneibothrium* **(Ec)** in the gonad of *Argopecten gibbus*. Numerous macrophagous hemocytes **(M)** surround the connective tissue capsule **(CT)** and nearby tissue. **OV** = ovarian acini containing developing eggs. Mallory's trichrome stain.

infestation appeared low, with 1–2 larvae observed per cm^2 section of gonadal tissue. Encysted larvae appeared surrounded by a connective tissue capsule of host origin and were located immediately subjacent to the wall of the gut. Each larva measured ~600 µm in length.

The presence of these organisms was accompanied by morphological changes in the intestinal wall tissue of *A. gibbus* in the vicinity of the cyst. The wall of the intestine normally consisted of a columnar ciliated epithelium separated by a basement membrane from a thin underlying layer of connective tissue (Fig. 2). Debris and sand particles were prominent features within the lumen of the intestine. Hemocytes were present in the sinus surrounding the intestinal loop, but were not normally present in great numbers between the gonadal acini at this stage of gametogenesis.

In contrast, the intestinal epithelium of parasitized scallops appeared to have undergone cellular change in which the normal ciliated columnar epithelium had been replaced by a stratified squamous epithelium, or undifferentiated cells. The lumen of the intestine contained sloughed epithelial cells and what appeared to be cellular debris and intact hemocytes (Fig. 3). In addition, hemocytes were abundant within the connective tissues of the gut wall and surrounding the acini of the gonads, although the germinal epithelium appeared identical to non-parasitized tissue and eggs did not differ significantly in diameter.

Differences in the gonadal dry weight indices were also observed among parasitized and non-parasitized

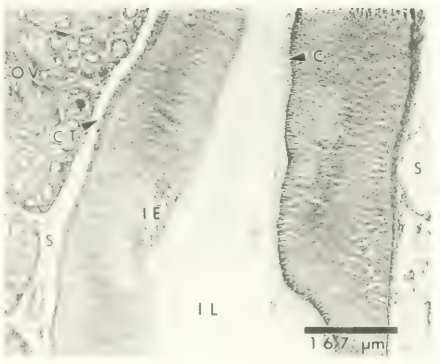

Figure 2

Cross-section of intestinal loop through gonad of unparasitized *Argopecten gibbus*. Note the ciliated columnar epithelium **(IE)**. Few macrophagous hemocytes are present in the hemolymph sinus **(S)** surrounding the intestine, and the lumen **(IL)** contains only a slight amount of particulate matter. **OV** = ovarian acini, **C** = cilia, **CT** = connective tissue. Mallory's trichrome stain.

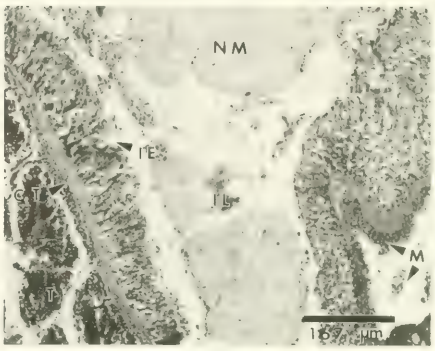

Figure 3

Cross-section of intestinal loop through gonad of a parasitized *Argopecten gibbus*. Note that the epithelium **(IE)** shows a loss of integrity, and the cells are more squamous than columnar. Ciliation has disappeared. The sinus surrounding the intestine contains numerous macrophagous hemocytes **(M)**. The lumen **(IL)** is filled with non-cellular debris **(NM)**. **T** = testicular acini, **CT** = connective tissue. Mallory's trichrome stain.

A. gibbus. The gonadal indices of non-parasitized *A. gibbus* during late gametogenesis and spawning were significantly higher (ANOVA, p=0.0001) than those of parasitized individuals in the same gametogenic state (Table 1).

Discussion

Past reports of larval *Echeneibothrium* hosts have been limited to species of *Venerupis staminea*, inhabiting the west coast of North America (Sparks & Chew 1966). Therefore, this report presents the first evidence for the occurrence of this genus in a bivalve from the east coast of North America, and the first indication of a scallop host. It is presently unclear how *Echeneibothrium* has

Table 1

Tukey's Studentized Range Test of mean gonadal indices (GI) among uninfected (January–April 1990) and infected (November 1990 and February 1991) *Argopecten gibbus* in the same reproductive state. Means not significantly different are underlined.

	Pairwise comparisons of GI					
	Feb '90	Mar	Jan	Apr	Feb '91	Nov
Mean	21.15	17.13	15.93	14.74	9.93	6.11
SD	±6.10	±2.96	±3.05	±4.28	±1.97	±2.08

migrated to eastern coastal waters. It is possible that parasitized intermediate and/or final host species either were introduced or migrated into the area.

Invasion of molluscan gonadal tissue by parasitic flatworms has been described as a secondary invasion, with the hepatopancreas (digestive gland) serving as the primary site. The resulting damage to the gonad, including atrophy and eventually destruction of the germinal epithelium, is believed to be a combination of mechanical pressure and nutrient deprivation (Cheng 1967). However, within the gonads of parasitized *Argopecten gibbus*, these changes were not apparent. Developing and mature eggs in the acini were identical in morphology to the eggs seen in non-parasitized tissue, and did not differ significantly in diameter (Singhas 1992). The only obvious difference was the higher numbers of hemocytes surrounding the germinal epithelium in infected scallops. The most extensive tissue damage in parasitized *A. gibbus* occurred in the epithelium of the intestinal loop. This damage consisted of alterations in intestinal epithelial cell shape and structural integrity, similar to those described by Cheng (1967) for hepatopancreatic tissue.

Failure of the local commercial crop of *A. gibbus* coincided with the appearance of *Echeneibothrium* in 1991 (P. Phalen, N.C. Div. Mar. Fish., Morehead City NC 28557-0769, pers. commun.). It is uncertain if the *Echeneibothrium* infestation contributed directly to this failure, because this species is known to undergo dramatic fluctuations in number (Moyer & Blake 1986). However, the commercial failure of *A. gibbus* in Florida during January–February 1991 was attributed to a Protoctistan parasite, *Marteilia* sp. (Blake & Moyer, 1992). Parasitism may therefore be an important factor in the population biology of *A. gibbus*, and merits further investigation.

Acknowledgments

We would like to gratefully acknowledge Dr. Thomas Cheng for his identification of the organism described in this Note, and for his editorial assistance with the manuscript. Thanks also to Dr. Charles Singhas for technical and editorial assistance, and to Dave Taylor of the N.C. Division of Marine Fisheries for his assistance in collections.

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Abstract. – An analysis of alternative methods for detecting trends in a series of abundance indices is carried out through simulation. The alternative procedures explored have been applied to analysis of relative abundance indices of dolphins in the eastern Pacific Ocean. They include a linear test over a moving time-period, and a nonparametric procedure based on smoothing of the time-series of abundance indices. Results indicate that the nonparametric procedure outperforms the linear tests in most of the situations tested.

A comparison of tests for detecting trends in abundance indices of dolphins

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An important part of the analysis of any set of abundance indices is the application of an objective procedure or test to determine whether changes in the estimates are due to random fluctuations in conditions of the sampling procedure or to actual changes in the population size. Such a procedure must exhibit certain properties in order to be effective. Among these properties, perhaps most important is the power of the test for a given significance level.

In deriving conclusions about changes in the size of a population, we can fall into two types of error. First, we can erroneously conclude that population size has changed when, in fact, differences in estimates are due to random errors. This is usually known as a Type-I error. A Type-II error occurs when we conclude that the estimates reflect random fluctuations when, in fact, there has been a change in population size. The probability of falling into a Type-I error is usually referred to as the significance level of the test. The power of a test is defined as 1 minus the probability of a Type-II error. An ideal test will minimize the trade-offs between both types of error. Another desirable property of a test is robustness to underlying assumptions about the populations. For example, tests commonly carried out to detect changes in population size are based on specific assumptions about the error structure of the estimates (e.g., normality) and the model that would best describe the population size as a function of time (e.g., linear, exponential; see, for example, Gerrodette 1987).

In the case of dolphin stocks involved in the tuna fishery in the eastern Pacific Ocean (EPO), it has been recommended that their management should include both estimates of absolute abundance, derived from research-vessel data (RVD), and analysis of trends in relative abundance, derived from tuna-vessel observer data (TVOD) (IWC 1992:218). In the case of EPO dolphin stocks, the use of TVOD seems the natural choice for analyzing trends, given the vast amount of low-cost information available from the observer programs. However, for this analysis to be effective, it is necessary to obtain abundance estimates with a constant bias over the years, or, at least, a bias that shows no trend over the years. Procedures developed by the Inter-American Tropical Tuna Commission (IATTC) to analyze the TVOD, described in Buckland & Anganuzzi (1988) and Anganuzzi & Buckland (1989), were specifically aimed at reducing the magnitude of year-to-year fluctuations in the estimates due to changing biases. These procedures were complemented with more specific analyses when there were reasons to suspect that biases might be changing, for example, due to widespread use of high-resolution radar for the detection of birds (Anganuzzi et al. 1991). However, in spite of the robustness of the methods, randomly fluctuating biases (an extra source of

variability) may still affect estimates from year to year. This problem may not be exclusive to the TVOD estimates; interannual variability also seems to affect estimates of relative abundance derived from research-vessel data (Wade & Gerrodette 1992). These biases and imprecise estimates will affect the performance of statistical tests designed to detect trends and, ultimately, our ability to draw conclusions about the status of populations.

For the analysis of trends in the EPO dolphin stocks, Buckland & Anganuzzi (1988) applied a linear test for trends over a moving period of 5 yr, although they expressed concern about the low power of such a test. Edwards & Perkins (1992) extended the moving time-frame to 10 yr to increase the power. However, such a test still shows some undesirable properties. Given the inadequacy of the tests based on linear regressions, Buckland et al. (1992) proposed a different procedure, based on a nonparametric regression, which addresses some of the problems exhibited by the linear test.

In this paper, the characteristics of these tests are discussed and compared by analyzing their performance in a number of simulated scenarios.

Current tests for trends

Linear tests

Buckland & Anganuzzi (1988) tested for linear trends over successive 5 yr periods by carrying out a weighted linear regression of abundance index vs. time. Each individual estimate was weighted by the inverse of its variance, calculated by applying a bootstrap procedure. The null hypothesis for the test is that no change has occurred in the population, i.e., that the slope of the regression is equal to zero. As the authors noted, the test has low power since it estimates precision from the deviations of only five estimates from a straight line. Power can be increased by extending the moving time-period to incorporate more years in the test. Unfortunately, this also increases the probability of violating the assumption of a constant rate of change implicit in the linear model being fitted to the estimates (Edwards & Perkins 1992).

The linear test also fails to consider the precision of estimates adequately. Variances of the estimates are not taken into account except as weights in the regression. As a consequence, only the ratios of the variances between estimates are relevant, and not their absolute values. For example, if for any given series of estimates we double the variance of each individual estimate, the results of the test will remain unchanged.

Weighting by the inverse of the variance can also present other problems. Suppose, for example, that the variance of the estimate is not independent of the estimate itself, but that the variance is correlated with the estimate, i.e., the coefficient of variation (CV=ratio of standard error to point estimate) is constant. In this case, a very low estimate (and especially in the case of an outlier) with a correspondingly small variance will become an influential observation. A linear test for trends will then indicate that there was a decline in the population if that estimate is at the end of the moving period, or a significant increase if it is at the beginning. An example from the EPO dolphin abundance estimation is the case of the 1983 index of relative abundance for the northern stock of offshore spotted dolphin *Stenella attenuata*, which was an anomalous index as a result of a very strong El Niño event (Fig. 1). In such cases, where the error distribution of the estimates seems to be better approximated by a lognormal distribution, it would be more appropriate to apply weights (wt) defined as

$$\mathrm{wt} = \ln(1+\mathrm{CV}^2)^{-1}. \qquad (1)$$

For the comparisons in this paper, two versions of the linear test are applied: the original 5 yr linear test with inverse variance weighting applied by Buckland & Anganuzzi (1988), and a 10 yr linear test with weights as described by Eq. 1.

Smoothed trends

The approach taken by Buckland et al. (1992) differs considerably from the method just described. First, they replaced the assumption of a parametric model for the underlying change in population with a nonparametric model. Among the many possible choices for such a model, they selected the smoothing algorithm known as '4253H, twice' (Velleman & Hoaglin 1981) on the basis of a comparison described by K. L. Cattanach and S. T. Buckland (SASS Environ. Model. Unit, MLURI, Craigiebuckler, Aberdeen, Scotland, unpubl. manuscr.). The adoption of a nonparametric model increases the robustness of the test to model misspecification, a problem that affects the linear test. Furthermore, the procedure, which involves the use of a compound running median, incorporates the information from nearby years into calculation of the smoothed estimate for a particular year, therefore reducing the influence of possible outliers and increasing the precision of each smoothed estimate. The smoothed test also provides a different way of looking at the trend. Instead of the trend being described by a single parameter (the slope of a linear regression), the sequence of smoothed estimates constitutes the best estimate of the underlying trend.

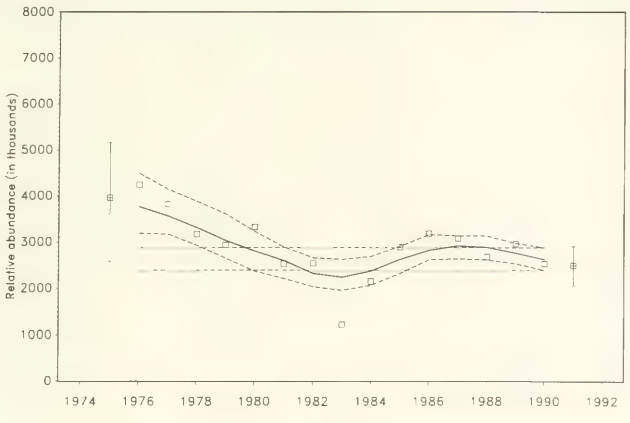

Figure 1

Smoothed trends in abundance of the northern offshore stock of spotted dolphin *Stenella attenuata* in the eastern tropical Pacific Ocean. Broken lines indicate ~85% confidence limits. Horizontal lines correspond to 85% confidence limits for the 1990 estimate. If both the 1990 confidence limits lie above the upper limit for an earlier year, abundance has increased significantly between that year and 1990 ($p<0.05$); if both limits lie below the lower limit for an earlier year, abundance has decreased significantly.

To obtain confidence intervals of the smoothed estimates, Buckland et al. (1992) combined smoothed estimates and bootstrap replication using the following procedure. First, they obtained 79 bootstrap estimates of the abundance index for each year. Next, they built bootstrap replicates of the series of estimates by taking, for example, the first bootstrap estimate for each year to obtain the first replicated series. They smoothed each replicated series, thereby obtaining 79 smoothed estimates for each year. Finally, they sorted the smoothed estimates within each year and obtained 85% confidence intervals based on the percentile method (Buckland 1984). The median of the smoothed bootstrap replicas is considered to be the best smoothed estimate.

The confidence intervals thus calculated allow a direct comparison between estimates. If the confidence intervals for two estimates do not overlap, then they are significantly different at a level of ~5%. An example based on estimates of relative abundance for the northern stock of offshore spotted dolphin is shown in Fig. 1. Since the last and first smoothed estimates are too variable, Buckland et al. (1992) recommend excluding them from the comparisons. The significance level is approximate, since it depends on normality of the estimates, homogeneity of the variances of estimates, and their independence. The second condition is often not met, but it can be shown that results are robust-to-moderate departures from it. The third condition is not met for estimates that are close in time, due to the correlation introduced by smoothing, and the relative importance of this effect is discussed further below.

Simulation comparison between tests

To illustrate the difference in performance between methods, a simulation study was carried out. Series of estimates were simulated by assuming different scenarios of underlying trends in the population over a period of 25 yr. The following scenarios were chosen.

Stable population Population exhibits no trend over the simulated period. This scenario provides us with an estimate of the probability of a Type-I error detecting a trend when, in fact, there is none, or obtaining a "false positive." Under this scenario, a percentage of detected trends close to 5% would be expected for a test based on a significance level of 5%.

Rapid decline Population remains at a constant level for a period of time, and then declines sharply over a period of 3 yr to 50% of its previous level. After the decline, the population recovers at a rate of 5% per yr.

Steady decline Population declines exponentially at an annual rate of 10%.

Steady cycle Population follows a sinusoidal change over the simulated period, completing one cycle over the 25 yr. Amplitude of the cycle is 30% of the original population size.

These scenarios are intended as a means of highlighting properties of the different tests and not as an exhaustive list of possible situations. Each scenario was replicated 100 times for different combinations of sources of variation. Variability in the estimates was assumed as coming from two different sources: (1) **Interannual variability**, resulting in a point estimate for each year t of

$$I_{0t} = N_t e^{\varepsilon},$$

where z is a random variable distributed as N (0, σ^2), and (2) **precision of the estimate**, represented in the distribution of the simulated bootstrap replicas for year t, I_{bt}, as

$$I_{bt} = I_t e^v, \text{ for b=1, . . ., 79,}$$

where v is a random variable distributed as N (0, ε^2).

The rationale for a setup with independent control of two sources of variation and a lognormal error structure lies in the properties of the estimates and in the fact that the linear and smoothed tests deal differently with both components of variation. The choice of a lognormal error structure can be justified by considering that the abundance estimates are naturally constrained to be positive. The choice of error structure for the simulation can be further justified by an analysis of the available TVOD estimates (Fig. 2), which shows that the main target stocks tend to have constant CV's, particularly in recent years when observer coverage of the tuna fleet increased and more information was available for abundance estimation. There is considerable variability in some stocks, due to changing levels of targeting from the purse-seine fleet that result in unequal sample sizes from year to year.

The argument for including two sources of variation in the estimates is based on the possibility that actual relative abundance indices are affected by random biases from year to year. Under standard assumptions, σ^2 and ε^2 should be equal. However, estimates of dolphin abundance may exhibit an additional variability, represented in this setup as $\sigma^2 > \varepsilon^2$. This can be attributed to randomly-fluctuating biases, such as those introduced by changing environmental conditions or differences in the way the purse-seine fishery operates. It is important to separate these two components since, for example, in the case of the linear test, the results are affected only by the variability represented by σ^2.

Therefore, it was assumed in the simulation that estimates are lognormally distributed around the underlying trend with a constant coefficient of variation. Figure 3 illustrates one simulated series for each of the different scenarios. The simulations were repeated for different combinations of CV_σ and CV_ε, the coefficients of variation for both sources of variation.

To compare the test for trends, two diagnostics were used.

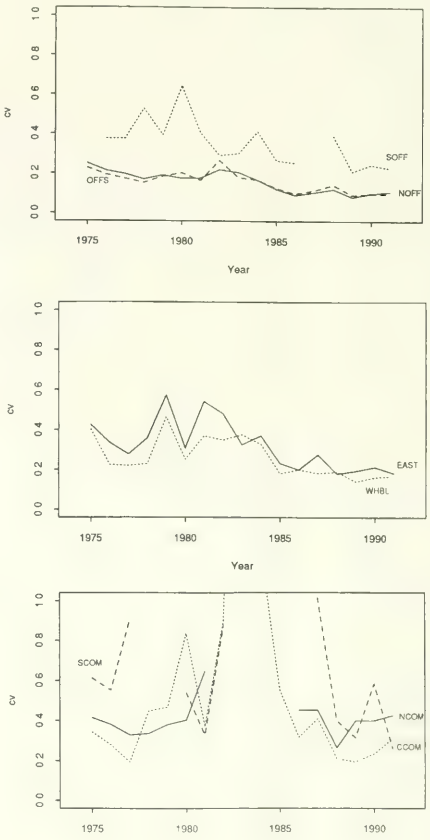

Figure 2

Coefficients of variation in relative abundance estimates of dolphin stocks in the eastern Pacific Ocean as a function of time. **NOFF**=northern stock of the offshore spotted dolphin *Stenella attenuata*; **SOFF**=southern stock of the offshore spotted dolphin; **EAST**=eastern stock of the spinner dolphin *Stenella longirostris*; **WHBL**=whitebelly stock of the spinner dolphin; **NCOM**=northern stock of the common dolphin *Delphinus delphis*; **CCOM**=central stock of the common dolphin; **SCOM**=southern stock of the common dolphin.

Number of detected trends For the linear trends, this is the number of 10 yr periods with slopes significantly different from zero at the 5% significance level. For the smoothed test, it is the number of significant differences between the next-to-last estimate and the estimate 10 yr earlier. In this way, the comparison is based on the same number of tests for each method. Since there are 25 yr simulated in each replica, a total of 1500 tests were carried out in the simulation of each scenario.

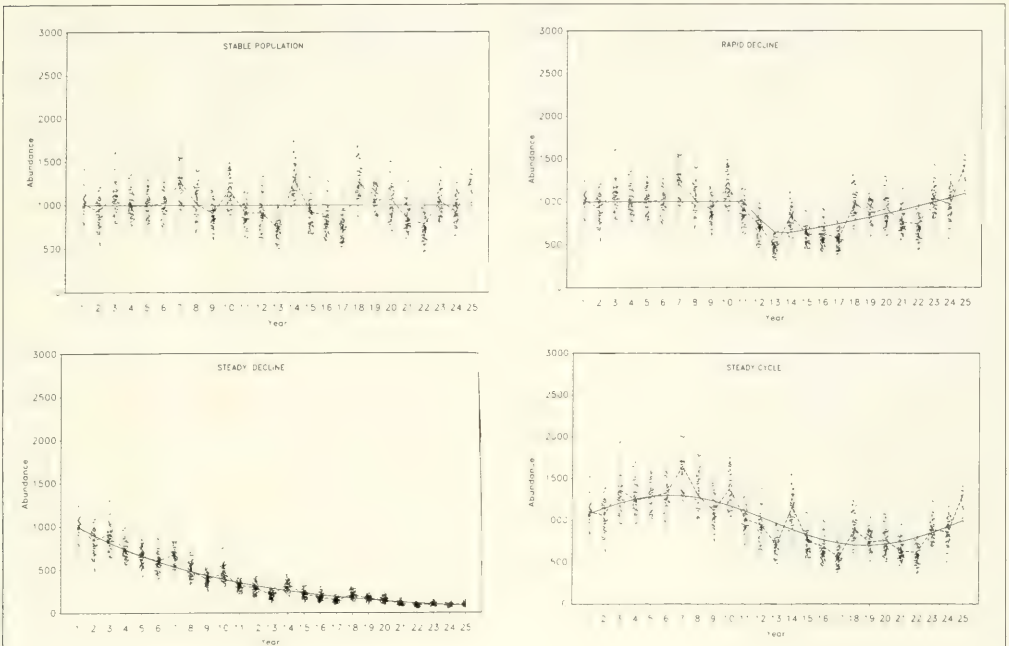

Figure 3

Example of a simulated series of relative abundance estimates for each of four scenarios. Solid line represents true underlying trend in the population. Dashed line connects simulated point estimates. Distribution of simulated bootstrap estimates is represented by the distribution of dots.

Ratio between estimates As a way of assessing how well each method describes the underlying trend in the population, an estimated rate of change was obtained. For the smoothed test, this is the ratio of two smoothed estimates separated by 10 yr. For the linear test, it is the ratio of the corresponding estimates calculated from the linear regression. These estimated rates of change were then compared with the true rates of change and the discrepancies summarized as average absolute error.

Correlation in the smoothed estimates

One of the problems of the smoothed test is that the smoothing procedure induces a correlation between estimates. This lack of independence affects the results of the comparison between estimates close in time, and it is therefore important to assess the magnitude of this correlation and how it is reduced as the separation in time between estimates increases. To investigate this, the following Monte Carlo procedure was carried out on the series of relative abundance estimates for dolphin stocks in the EPO reported by Anganuzzi et al. (1992).

1 For each year, 79 estimates were sampled with replacement from the distribution of bootstrap estimates of relative abundance. The 79 estimates were available from the standard bootstrap procedure used to estimate confidence bounds in the relative abundance estimation (Anganuzzi & Buckland 1989).

2 Each of the 79 trajectories obtained in the previous step were smoothed, and 85% confidence limits for the resulting smoothed estimates were obtained based on the percentile method. This step is essentially the application of the smoothed test.

3 Steps 1 and 2 were repeated 100 times, therefore obtaining 100 estimates of the lower and upper confidence bounds for the smoothed estimates for each year.

4 A correlation matrix between years for both upper and lower limits of the confidence bounds was estimated on the basis of results of the previous step.

5 Estimates of correlation as a function of the distance in time between estimates were obtained. This was done by averaging over all correlation coefficients between estimates separated by a given number of years, that is, by taking the average of elements in the subdiagonals of the correlation matrix obtained in step 4.

Results

Number of detected trends

The results of this analysis are shown in Figs. 4–7, as the number of detected trends each year in 100 simulations for the different scenarios. The underlying trends are shown on an arbitrary scale to relate changes in performance of the tests to changes in population trajectory.

Stable population This scenario can be used to assess the actual level of significance of the tests. An ideal procedure for detecting trends would indicate significant trends in ~5% of the tests under this scenario, given that the significance level is set at 5%. Results from the simulations are shown in Fig. 4. Both linear tests show an actual significance level close to the expected value. These results were relatively robust to the different values of CVs tested. The smoothed test also performs well in all cases, except when interannual variation exceeds the precision of the estimate. For example, for CV_σ=0.2 and CV_ϵ=0.3, the percentage of detected trends was ~10%.

Rapid decline In this scenario, different trade-offs of the tests are illustrated by their performance along the simulated period (Fig. 5). For CV_σ=CV_ϵ, at the beginning of the period both the linear and smoothed tests have similar proportions of detected trends, close to the nominal significance level. As the underlying trend in the period included in the tests departs from linearity, the smoothed test tends to outperform both linear tests. For CV_σ=CV_ϵ=0.2, the smoothed test indicates a maximum of almost 80% significant trends in

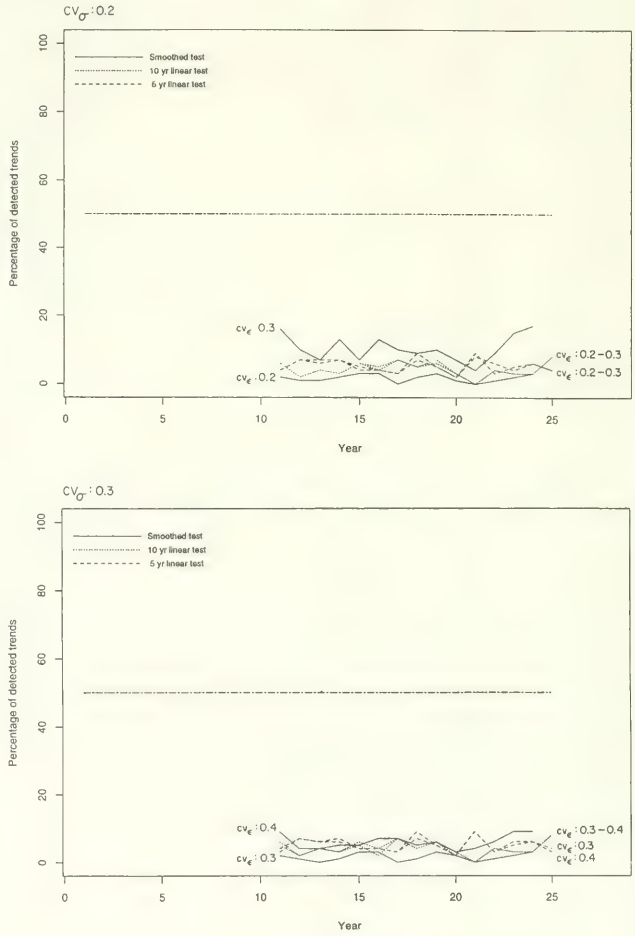

Figure 4

Percentage of trends detected in 100 simulations of the **'stable population'** scenario for two levels of precision: **(top)** CV_σ=0.2, and **(bottom)** CV_σ=0.3. The two lines for each smoothed test represent different levels of interannual variation, CV_ϵ. Broken line (– – –) represents underlying trend in the population on an arbitrary scale.

comparison with <60% for the linear test. In the recovery phase of the trajectory (starting when the tests cover the period between years 12 and 22), the linear test improves its performance relative to the smoothed test. In absolute terms, the performance of both tests seems to be poor between years 20 and 23, but this is the result of the small difference between the first and last year of the period included in the moving timeframe. After that, the 10 yr linear test performs almost as well as the smoothed test, as the result of an underlying trend that can be approximated well by a linear model. The 5 yr linear test does not perform well, although it detects the decline more frequently than the 10 yr test. In spite of the improvement in the last part of the trajectory, both linear and smoothed tests reach a maximum of only ~70% of significant trends. The performance of all tests degrades quickly for higher amounts of variability; the maximum percentage of detections for the smoothed test falls to around 40% for CV_σ=CV_ε=0.3.

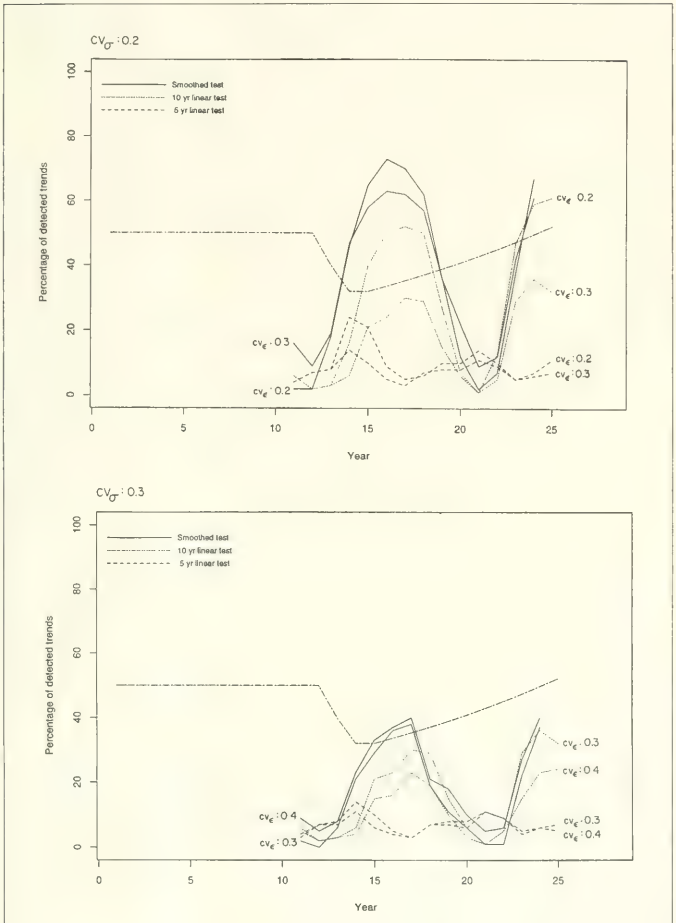

Figure 5

Percentage of trends detected in 100 simulations of the **'rapid decline'** scenario for two levels of precision: **(top)** CV_σ=0.2, and **(bottom)** CV_σ=0.3. The two solid lines for each smoothed test represent different levels of interannual variation, CV_ε. Broken line (– – –) represents underlying trend in the population on an arbitrary scale.

In the case of the smoothed test, the number of detections increases when CV_σ>CV_ε. This result seems to be a consequence of higher Type-I error probabilities, as suggested by the higher number of detections in years 11 and 12.

Steady decline The power of both types of tests improves under this scenario relative to the previous one, due to the smoother nature of the underlying trend (Fig. 6). For CV_σ=CV_ε the smoothed test outperforms the linear tests for all levels of variability. The percentage of significant trends detected by the smoothed test ranges from over 95% for CV's of 0.20 to ~80% for a CV of 0.30. The power of the 10 yr linear test seems to be more affected by increasing variability in the estimates, falling to ~50% detections for CV=0.40. For CV_σ>CV_ε, the power of the smoothed test seems to increase although, as before, this is probably the result of greater Type-I error rates. The 5 yr linear tests show low power for all levels of variability.

Steady cycle The results of this set of simulations are very similar to those from the 'rapid decline' scenario (Fig. 7). Overall performance for both tests im-

proves relative to that scenario, due to the smoother underlying trend, reaching a maximum of 90% for the smoothed test for CV=0.2. This performance falls rapidly, as the amount of variability increases, to a maximum of slightly over 20% when CV=0.40. For $CV_\sigma > CV_\varepsilon$, the smoothed test again shows an apparent increase in power related to high Type-I error probabilities. Once more, the 5 yr linear test shows very low power throughout the series.

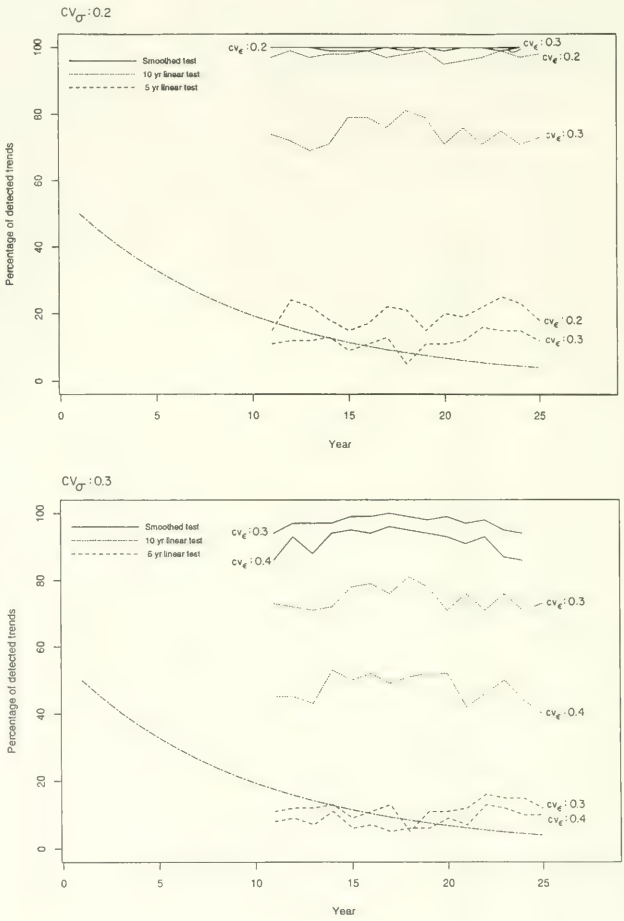

Figure 6

Percentage of trends detected in 100 simulations of the **'steady decline'** scenario for two levels of precision: **(top)** CV_σ=0.2, and **(bottom)** CV_σ=0.3. The two solid lines for each smoothed test represent different levels of interannual variation, CV_ε. Broken line (– – –) represents underlying trend in the population on an arbitrary scale.

Ratio between estimates

The purpose of this analysis is to assess sensitivity of the estimated rates of change, obtained by smoothing or linear procedures, to departures from linearity of the underlying trend. It also measures the ability of the procedures to reconstruct the true underlying population trajectory. The results of this analysis are shown for each of the simulated trajectories in Fig. 8. Results indicate that the estimated rates of change obtained through the smoothing procedures are better, in terms of the average absolute error, than estimates obtained by any of the linear methods, even when the simulated trend is linear ('stable' scenario, Fig. 8, page 192). Estimates from the 5 yr linear regressions are consistently worse than estimates from the 10 yr regressions, as expected due to the greater number of points on which the latter is based. The only exception is for the scenario with cyclic fluctuations, where the 10 yr linear estimates are poorer than the 5 yr estimates. This is a consequence of the period of the sinusoidal cycle in the underlying population that can be better approximated by a linear model over a short period of time. For longer periods in the cycle, 10 yr linear estimate should improve, as suggested by its performance in the scenario with an exponential decline. Results for the smoothed procedure are consistent over the sets of scenarios, indicating its robustness to departures from linearity in the population trajectory.

Correlation between smoothed estimates

Results from this analysis are shown in Figs. 9 and 10 (pages 193, 194), which indicate that the correlation

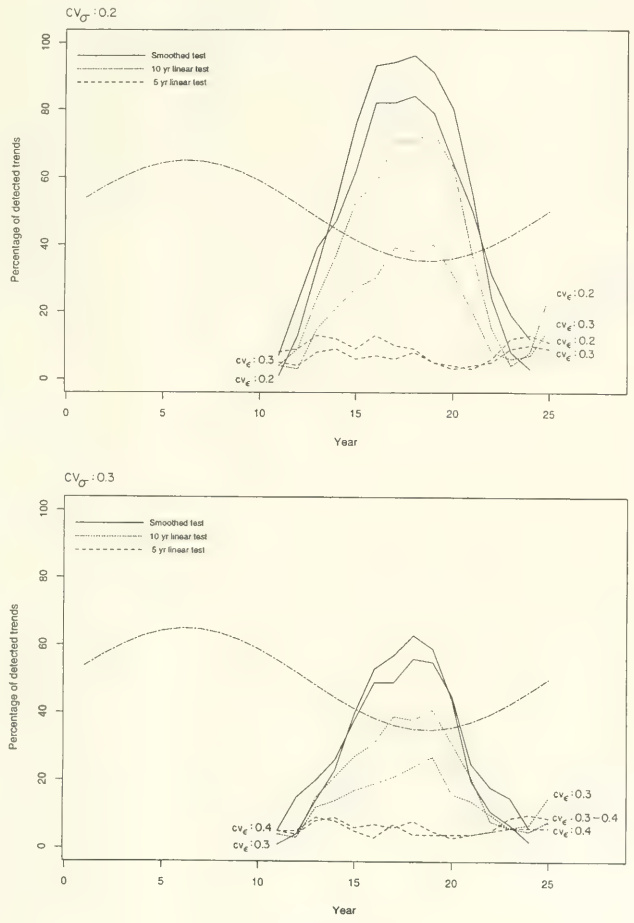

Figure 7

Percentage of trends detected in 100 simulations of the **'steady cycle'** scenario for two levels of precision: **(top)** CV_σ=0.2, and **(bottom)** CV_σ=0.3. The two solid lines for each smoothed test represent different levels of interannual variation, CV_ϵ. Broken line (– – –) represents underlying trend in the population on an arbitrary scale.

declines rapidly as distance between the estimates increases, approaching very low values as the separation between estimates exceeds 4 yr. This suggests that the validity of the test will not be seriously compromised by the correlation induced from the smoothing procedure, when the comparison is carried out on estimates that are separated by at least 4 yr.

A characteristic of the smoothed test is that, while the smoothing procedure induces a correlation between estimates, the correlation across years between fixed percentiles of the distribution of smoothed estimates is lower. This is a result of the (implicit) sorting of estimates that removes some of the dependency. To illustrate this, the average correlation between smoothed estimates obtained before sorting is also shown in Figs. 9 and 10, suggesting that the reduction in correlation due to sorting is ~30% for estimates close in time.

Discussion

In summary, the two types of tests represent different ways of looking at the data, and a comparison between them based on the same criteria only partially reflects these differences. The smoothed test provides more information since it allows a graphic comparison between individual estimates. It is based in a more robust assumption about the underlying trend of the population, since it assumes only that the change has been smooth over a short time-period. It also incorporates the lack of precision of the estimates in a much more effective way than the linear test.

In some cases, however, the linear test might be more suitable. For example, if the amount of interannual variation is low relative to the precision of the estimates, or if changes are closely approximated by a linear function, the linear test should perform better. Also, if large changes in population size occur over a very short time-period, smoothing the series will tend to underestimate the rate of change.

Despite limitations of the comparison, the results from simulations indicated that the smoothed test outperforms the linear test in most situations. The only exception is the tendency to detect spurious trends

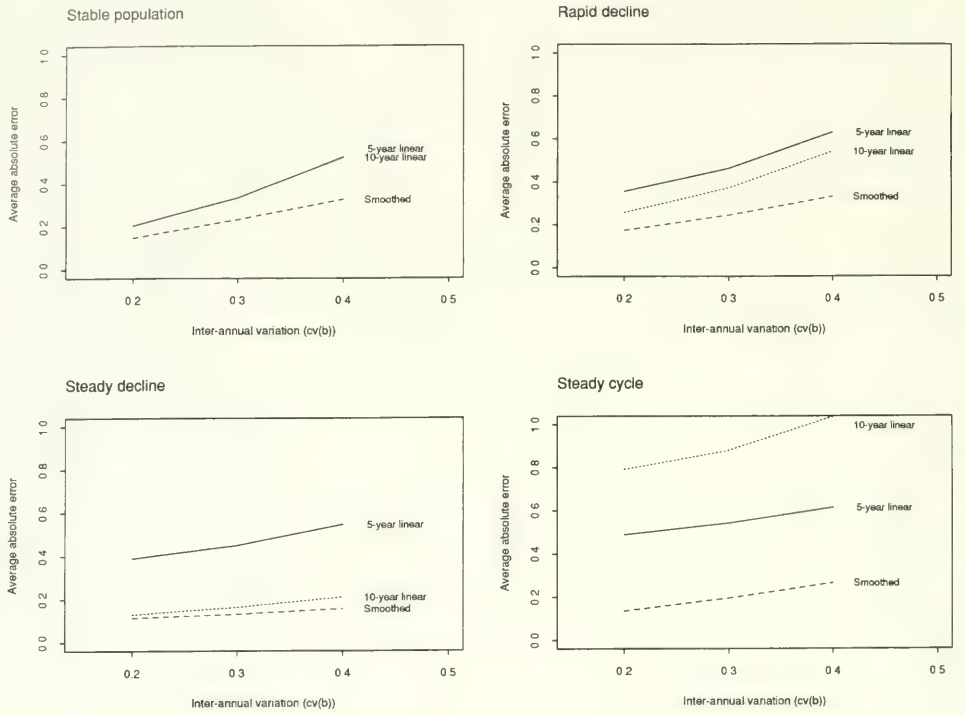

Figure 8

Average absolute error as a function of different degrees of interannual variation, represented by CV_b, for each of the four scenarios simulated.

when the amount of interannual variability exceeds precision of the estimates. In other words, in the inevitable trade-off between Type-I and Type-II errors, the smoothed test has lower Type-II error rates at the expense of an increase in the Type-I error rate. From the management point of view, this is a safer compromise than the one posed by the linear test, since the probability of failing to detect a significant trend is smaller with the smoothed test. The increase in Type-I error rates can be related to the amount of smoothing done by the particular algorithm chosen. An algorithm that would smooth the estimates more would be less prone to this problem, but it would have less power to detect trends in the estimates in certain situations. Such an algorithm would also induce more correlation between smoothed estimates, and the separation in time between them would have to be greater in order not to compromise validity of the comparisons. An alternative would be a smoothing algorithm that can adaptively change the amount of smoothing done on the estimates, either by cross-validation techniques or by controlling the amount of smoothing through incorporating auxiliary information, such as birth and death rates, in the procedure; in other words, by building a model of the population dynamics.

Acknowledgments

I would like to thank Bill Bayliff, Steve Buckland, Martin Hall, and Tim Gerrodette for their valuable comments.

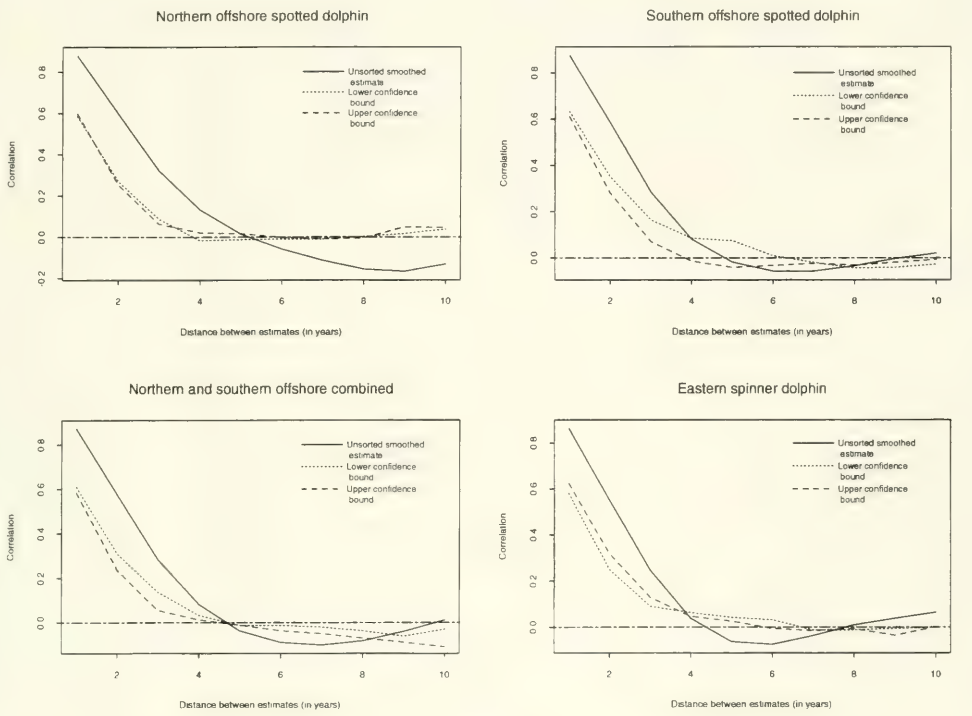

Figure 9

Correlation between smoothed estimates as a function of the separation in years between estimates for four stocks of dolphin in the eastern Pacific Ocean: Offshore spotted *Stenella attenuata* and spinner dolphin *Stenella longirostris*.

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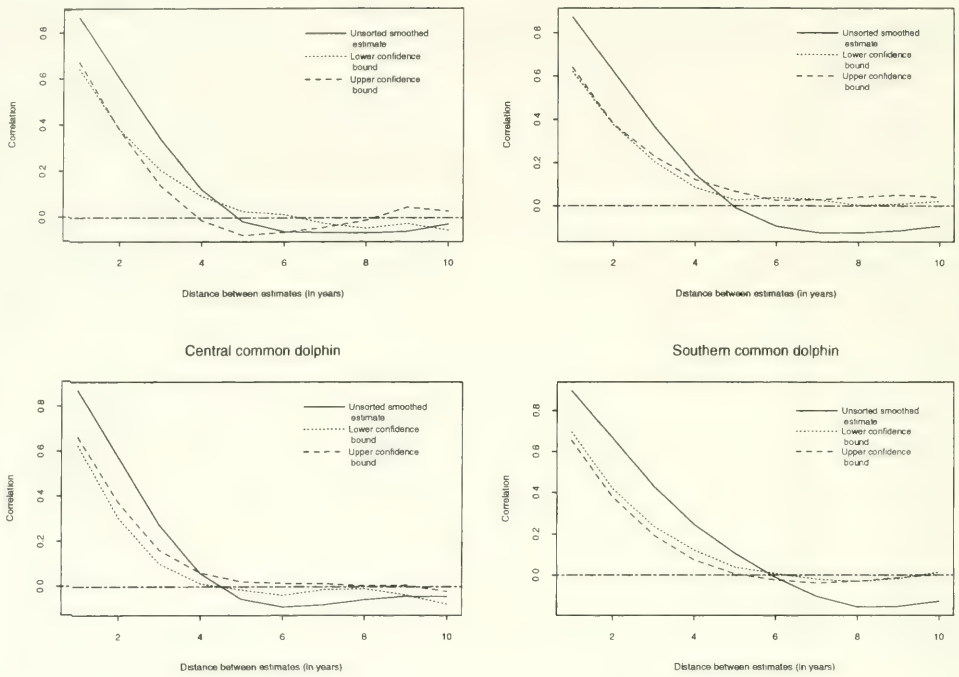

Figure 10

Correlation between smoothed estimates as a function of the separation in years between estimates of four stocks of dolphin in the eastern Pacific Ocean: Spinner dolphin *Stenella longirostris* and common dolphin *Delphinus delphis*.

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A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes*

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Abstract. – We compared sampling performance of four nets and two aggregation devices for larval and pelagic juvenile coral-reef fishes. The six sampling devices were deployed simultaneously over three nights near a coral reef at Lizard Island, northern Great Barrier Reef, Australia. The resulting 83 samples captured 57,701 larval and pelagic juvenile fishes of 70 families (excluding clupeoids which were not considered in this analysis). The bongo net took the most families, and the light-trap the fewest. In all methods, a few families dominated the catch. Dominance was least in the Tucker trawl catches and greatest in light-trap catches, where pomacentrids constituted 93% of the catch. Composition of catches was similar for the four nets. Catches from the light-trap were markedly different from those taken by net; catches taken by light-seine showed similarities to those taken by both net and light-trap. For four abundant families (Apogonide, Gobiidae, Lutjanidae, Pomacentridae), the bongo net gave the overall highest density estimates, although those from purse-seine were frequently equivalent to bongo-net estimates. The Tucker trawl provided the lowest density estimates in most cases. Catches of bongo, neuston, and seine nets were similar in size structure and were dominated by small larvae; overall, however, bongo nets collected the greatest size-range of fishes. The Tucker trawl did not collect small larvae well nor did it collect significantly greater densities of large larvae and pelagic juveniles than the bongo net. Fishes collected by aggregation devices were generally larger than those taken by net, and light-traps caught very few fish <5 mm. Light-traps collected greater numbers of large pomacentrids (>6 mm) than other methods. In an extended sampling period of five nights, both aggregation devices showed obvious peaks in the density of large pelagic pomacentrids and mullids; these patterns were not detected by the nets.

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Almost all species of marine teleost fishes have a pelagic phase in the early part of their life history (Moser et al. 1984). Size, morphology, and behavior of larval and pelagic juvenile phases vary greatly (Moser 1981), and this makes accurate sampling of these fishes problematical (Murphy & Clutter 1972, Frank 1988, Suthers & Frank 1989, Brander & Thompson 1989). The problem is exaggerated in tropical waters due to high taxonomic and developmental diversity and the presence of many demersal species with extended pelagic phases (Leis & Rennis 1983, Leis & Trnski 1989, Leis 1991b). Studies of the pelagic phase can provide important information on population biology of reef fishes. Despite its brevity, the high mortality and dispersion characteristic of this phase can have important demographic consequences for many species (Victor 1986). There is now a widespread interest in the process of recruitment in coral reef fishes (Doherty & Williams 1988, Warner & Hughes 1989), and sampling techniques which cover the full size-range of the pelagic phase are needed.

A number of different methods are available to sample this complex assemblage of early-life-history stages, including towed nets, purse-seines, and various types of aggregation devices which attract fish into collection sites or traps. These methods differ in their method of deployment and capture, and each has its own set of advantages and disadvantages. All have biases in number, identity, and sizes of pelagic fishes collected (Clutter & Anraku 1968, Clarke 1983 and 1991). For the pelagic phase of reef fishes, there have been few attempts to evaluate the relative bias of different sampling methods. Recent studies have provided information on the comparative performance

*Contribution of the Lizard Island Research Station. Authorship alphabetical.

of nets and light-traps (Gregory & Powles 1988), nets and plankton pumps (Brander & Thompson 1989), and towed nets and purse-seines (Kingsford & Choat 1985), but have dealt with the less-diverse fauna of temperate waters.

The purpose of this study was to compare several types of towed and seine nets and an automated light-trap (Doherty 1987) in terms of taxa, numbers, and sizes of larvae and pelagic juveniles of coral reef fishes captured. These methods represent the range of sampling devices currently used to collect larval and pelagic juvenile fishes. For the towed nets, we used dimensions and mesh size normally employed to sample larval and pelagic juvenile fishes. We used designs of purse-seine and light-trap which had been subject to thorough field testing (Kingsford & Choat 1985 and 1986, Kingsford et al. 1991, Doherty 1987). For each sampling device we obtained the following information: (1) Taxonomic composition of samples at the level of family; (2) patterns of density and size structure in selected taxa; and (3) temporal patterns in the density of selected taxa over short time-periods. The program also provided information on the logistic constraints associated with each sampling method.

Our findings will be useful to those designing sampling programs for larval and pelagic juvenile stages of demersal fishes in tropical and other areas, and should have some generality because the taxa sampled included a wide variety of body shapes and swimming capabilities. Among the taxa studied are families of great importance in coral reef ecosystems as adults (Apogonidae, Atherinidae, Callionymidae, Gobiidae, Labridae, Pomacentridae), and several are also important in commercial, sport, or subsistence fisheries throughout the tropics (Carangidae, Lethrinidae, Lutjanidae, Mullidae, Nemipteridae, Platycephalidae, Scaridae). All are abundant in ichthyoplankton samples in tropical coastal areas, especially in the Indo-Pacific.

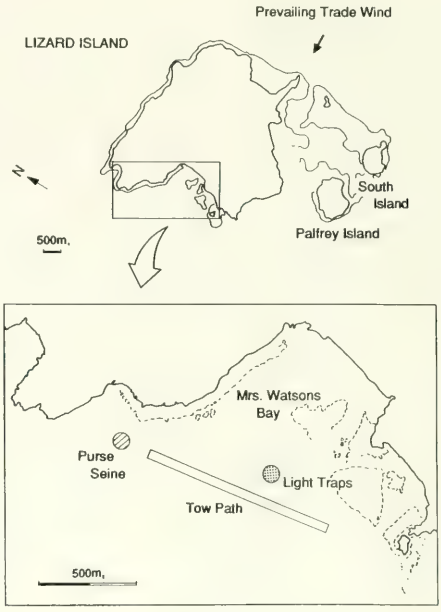

Figure 1

Lizard Island, Great Barrier Reef, Australia, showing location of study area and position of sampling sites for light-traps, towed nets, and purse-seines at Watsons Bay. Coral reefs are shown as broken lines. Lizard Island (145°26'E, 14°40'S) is located 30 km off the eastern coast of mainland Australia.

Materials and methods

Sampling and identification procedures

We sampled at 150–600 m off the fringing reefs at Watsons Bay on the NW side of Lizard Island in the lagoon of the northern Great Barrier Reef, Australia (145°26'E, 14°40'S). Water depth was 20–30 m over a sandy bottom (Fig. 1). This site was chosen for its proximity to the logistic support offered by the Lizard Island Research Station, a base for much work on the pelagic phase of coral reef fishes (Leis 1991b). Also, it offered relatively sheltered conditions from the 15–25 kn southeasterly winds present during the sampling period. This was particularly important for the continuity of sampling over a number of nights.

We sampled on the nights of 2, 3, 5, 6, and 7 December 1986, starting at a minimum of 1.25 h after sunset. Sampling never continued past 0200 h. New moon was on 2 December 1986. Nocturnal sampling reduces potential bias due to vertical distribution because ichthyoplankton show little vertical stratification at night in the study area (Leis 1986, 1991a). In addition, the nets should operate at peak efficiency at night due to lessened visual avoidance. Finally, the aggregation devices are effective only at night because they depend on self-generated light to attract fishes.

We concentrated our analyses on data from 3, 5, and 6 December because we were able to take and process all planned samples from all gears only on these nights. For some gears, it was possible to examine temporal trends over the full sampling period.

Six different sampling devices were deployed each night. Three nets were towed from the 14 m catama-

ran RV *Sunbird* at 1 m/s along a fixed 1 km path. The towed nets were fitted with flowmeters and were washed with pumped seawater. Details of each collection device are as follows.

1 A neuston net of mouth dimensions 1.0×0.3 m with 0.5 mm mesh was rigged to sample water between the bows of the catamaran. Typically, the net sampled to a depth 0.1 m and filtered 187–312 m^3/tow. Four tows were taken per night.

2 A bongo net (McGowan & Brown 1966) of 0.85 m mouth diameter per side, and with 0.5 mm mesh, was towed from an "A"-frame at the stern. The RV *Sunbird* draws 1m, and the net was towed so its top was 1m below surface and on the vessel's centerline in water which had not been disturbed by the passage of its twin hulls. The volume of water filtered for each side of the net was 498–673 m^3/tow. Samples from only the port-side net were analyzed. Four tows were taken per night.

3 A Tucker trawl (Tucker 1951) with nominal mouth dimensions of 2×2 m and of 3 mm mesh was towed in the same position as the bongo net. At a towing speed of 1 m/s, a diver estimated that the bottom bar of the net trailed the top bar by ~0.5 m, so the effective mouth area was ~3.8 m^2. Between 3240 and 4570 m^3 of water were filtered per tow. Four tows were taken per night. Both the bongo net and the Tucker trawl used the same depressor.

Time constraints and the logistics of rigging and deploying each net precluded randomising the order of bongo and Tucker trawl tows, so they were taken in blocks of four, with the order alternating from one night to the next. Neuston net samples were taken during the Tucker trawl tows.

4 A plankton mesh purse-seine of 14×2 m (Kingsford & Choat 1985) of 0.28 mm mesh was used to take samples of ~32 m^3 each. This estimate was based on the ideal cylinder of water enclosed by the net at the beginning of pursing and made no allowance for herding of fishes during deployment or loss during pursing. There was no estimate of variation in the volume enclosed by the net sets. The net was deployed from a 4 m dinghy adjacent to the northern end of the tow path (Fig. 1). Wind conditions precluded effective deployment of this net at greater distances offshore. Two to four samples were taken per night.

5 Two automated light-traps (Doherty 1987) were deployed from an anchored boat adjacent to the center of the tow path and ~700 m from the purse-seine site. Traps were positioned at ~10 m apart. Entries into the trap were at 0.5–1 m below surface. The second trap began to sample 30 min after the first, and both traps sampled for hourly intervals, resulting in continuous sampling in overlapping, 1 h segments. The trap deployment was staggered to allow for clearing and processing of each trap after the 1 h fishing period. Eight to nine 1 h light-trap samples were taken per night.

6 A battery-powered fluorescent light source identical to that in the trap (Doherty 1987) was deployed from a second boat anchored at the purse-seine site. After 1 h in the water, the light was set adrift and the water around it immediately sampled by the same purse-seine used in **(4)** above. Our estimates of what was attracted to the light included only those individuals that were within ~2 m (i.e., radius of the seine at pursing) of the light at the time of seining. Four to five light-seine samples were taken per night. Purse-seine (no light, **(4)** above) and light-seine samples were interspersed during the night.

Our goal was to sample simultaneously using six methods in the same location over several nights, so as to avoid confounding comparisons of methods with temporal or spatial variation. The purse-seine, light-seine, and light-trap samples were taken throughout the nightly sampling period. At the same time, the RV *Sunbird* sampled with the towed nets. Logistic problems required two compromises in this program. Bongo tows and Tucker trawl tows (and simultaneous neuston tows) were done in sequential blocks of four each night as discussed in **(3)** above. The purse-seine and light-trap samples were taken 700 m apart because it was not possible to duplicate these devices and thus randomize their positions. The RV *Sunbird* tow track covered the area between these two.

Fishes from the towed nets, purse-seines, and light-seines were immediately fixed in 10% formalin seawater. Samples from the light-traps were maintained alive until returned to the Research Station where they were subsequently fixed in 100% ethanol or 10% formalin seawater. All fish were transferred to 70% ethanol for at least a month prior to measurement.

For light-traps and light-seines, density is expressed as number per sample. Catches from the towed net and purse-seine collections were standardized to the number of fishes/1000 m^3 on the basis of flowmeter records or purse-seine geometry.

All fishes were removed from samples and identified to family following Leis & Rennis (1983) and Leis & Trnski (1989). Standard lengths were measured to the nearest 0.1 mm using a Bioquant software package that allows for measurement of enlarged *camera lucida* images of fish and accommodates curvature of specimens. The accuracy of electronic measurement was monitored by measuring subsamples manually with calipers and eye-piece micrometers. In a few samples with very large numbers of certain taxa such as gobiids, the catch was subsampled and a minimum of 10% of the sample measured. For some analyses, fishes were divided into small (<6 mm) and large (≥6 mm) size-groups. This was done because, on the basis of results reported here, the light-

trap captures few larvae <6 mm, and we wished to compare density estimates among gears for the sizes of fishes captured by the light-trap. Damaged fish (~3% of total) were excluded from the length analysis.

The terminology of early-life-history stages of fishes is complex and ultimately arbitrary, whether based on morphological or ecological criteria (Kendall et al. 1984, Kingsford 1988, Leis 1991b). We were primarily interested in taxa of which the adults are benthic on coral reefs, but did not want to exclude semipelagic reef-associated taxa by use of an ecological term like 'presettlement', nor did we wish to exclude partially- or fully-transformed but still pelagic individuals of benthic taxa by the use of a morphological term like 'larva'. Therefore, we use the terms 'larvae' and 'pelagic juveniles' for the fishes collected during this study, or refer to them collectively as 'pelagic fishes'.

Larval, transforming, juvenile, and adult clupeoid fishes of several types (including *Spratelloides* spp., *Dussumeria* sp., *Stolephorus* sp., and probably *Herklotsichthys* sp.) were captured in large numbers, mainly by light attraction. These clupeoid fishes represented a distinct assemblage of fishes with a different age and size structure and adult habitat than the reef species of primary interest to us. These clupeoids are not considered here, but will be dealt with in a separate publication.

Reduction of data sets and analytical procedures

Sampling produced a data set comprising 70 families of fishes (exclusive of the Clupeidae and Engraulidae) collected from the sampling nights of 3, 5, and 6 December by six methods. For ease of analysis and unambiguous interpretation, it was necessary to reduce the number of families treated. We initially removed from consideration any family which did not constitute at least 1% of the catch of at least one method. The removal of taxa of this level of rarity would be unlikely to influence the outcome of the analyses (Green 1979). This excluded 51 families, leaving 19 (referred to as 'abundant families') for analysis beyond simple listing of numbers of families sampled (e.g., Table 1). Relative-abundance information obtained by all six sampling methods for the 19 abundant families was subjected to Principal Component Analysis (PCA) using the variance-covariance matrix. As a check, the same analysis was run incorporating the next 10 most-abundant families; this generated identical patterns. Reducing the data set from 29 to 19 families did not change the resulting pattern.

The PCA analysis identified patterns in the complex data set of 19 families sampled by six methods. Many of these 19 families were relatively rare and contributed little to the variation in the data set. A detailed examination of the factors contributing to these patterns required factorial analyses such as multivariate analysis-of-variance (MANOVA). These procedures are best carried out with a reduced number of variables, which allows a clearer interpretation of trends in the data. This called for a further reduction in the number of families analyzed.

To achieve this reduction, the data set of 19 families collected by nets was subjected to a PCA, which identified the taxa that contributed most substantially to the variation in the data set. This PCA identified apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids as major contributors (95.2%) to the variation in the data set. These six taxa were used in a MANOVA. This design provided sufficient degrees of freedom for testing and interpreting the significance of method and night of sampling. The analysis was carried out on samples from nets only.

For graphic display of trends in sampling by nets, the eight most-important taxa from the PCA were depicted. These were apogonids, atherinids, gobiids, lethrinids, lutjanids, mullids, pomacentrids, and labrids. Labrids were included in this group at the expense of schindleriids, as they were an abundant reef-associated taxon of considerable interest to reef fish biologists. This substitution did not affect the cumulative variance accounted for by the eight families.

Unlike nets, aggregation devices did not allow for adjustment of fish densities to a common volume. Moreover, aggregation devices collected a different set of fishes. An additional PCA run on light-trap and light-seine data identified atherinids, gobiids, labrids, lethrinids, mullids, and pomacentrids as taxa, which explained over 90% of the variability in the data set. The families selected showed a strong relationship to the overall abundance ranking, although two relatively rare taxa (lethrinids and mullids) were included.

Aggregation devices sample an unknown volume of water. Because catches by aggregation devices could not be standardized to number of fish per unit volume, we made separate comparisons of nets and aggregation devices. The variables used were mean number/1000 m^3 for nets, and mean number/sample for aggregation devices. A factorial analysis was designed to test for differences in sampling method (fixed) and time (random). For factorial analyses, residual analysis was performed (Snedecor & Cochran 1980) to check assumptions of normality and homogeneity of variance. Taylor's Power Law (Taylor 1961) was used to determine the appropriate transformation.

Canonical Discriminant Analysis and Tukey's Studentized Range Test (HSD) were used to display the differences detected. For MANOVA, the multivariate test statistic (Pillai's Trace) was used because it is

less likely to involve Type-I error and is more robust to heterogeneity of variance than comparable tests (Green 1979). All analyses were performed using SAS Version 6 (SAS 1987).

A more subjective procedure was used to select taxa for size-frequency measures. For meaningful comparisons, it was necessary to select taxa that were well represented in the collecting devices and that covered a reasonable size-range (>8 mm) within each method. Apogonids, gobiids, lutjanids, and pomacentrids met these criteria and also accounted for over 95% of the variation in the main data set from net sampling. Catches for nets and aggregation devices were analyzed separately. For net catches, density was expressed as mean number/1000 m^3 within 2 mm size-classes among the different methods and compared by one-way ANOVAs. With aggregation devices, the variable was the number of fish per sample and comparisons were made by *t*-tests.

Results

The 83 samples contained a total of 57,701 fishes of 70 families, excluding clupeoids (Table 1). Table 2 lists families which constituted at least 1% of the individuals taken by any sampling method and records their size-ranges by method. We refer to these as 'abundant families'.

Taxonomic composition and size structure of the samples

There were marked differences in taxonomic composition of the samples among methods. The bongo net collected the largest number of families overall (Table 1), including all of the abundant families and a wide size-range within most families (Table 2). The light-trap collected the fewest families overall and only

Table 1

Number of samples, total individuals, and numbers of families of fishes (clupeoids excluded) taken by six sampling methods on the nights of 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Volume of water sampled by aggregation devices is unknown.

Sampling method	Number of samples	Number of fish	Volume of water sampled (m^3)	Number of families
Light-trap	26	7624	unknown	20
Seined light	14	2707	unknown	37
Purse-seine	7	812	224	25
Neuston net	12	2418	2861	31
Bongo net	12	43417	6833	63
Tucker trawl	12	723	47100	29
Total	83	57701	—	70

Table 2

Numbers and size ranges of the 19 families of fishes which made up >1% of the catch of at least one method on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Clupeoids are excluded. Size-range in mmSL, and total number of individuals within the taxon (*n*).

	Sampling method											
	Light-trap		Light-seine		Bongo net		Purse-seine		Neuston net		Tucker trawl	
Family	SL	*n*	SL	*n*	SL	*n*	SL	*n*	SL	*n*	SL	*n*
Apogonidae	5.4–9.3	4	1.6–9.8	211	1.6–15.5	10295	1.6–6.8	86	1.7–6.2	491	2.3–5.1	99
Atherinidae	6.7–19.1	20	7.6–61.7	135	6.0–25.2	14	6.8–24.7	2	16.0–56.3	110	15.2–39.3	36
Bothidae			3.2–5.3	3	1.4–7.7	76					3.0–10.0	10
Callionymidae			1.3–3.5	35	1.1–4.9	1003	1.3–2.9	11	1.6–3.9	94	1.9–4.5	6
Carangidae			1.9–57.4	19	1.8–7.6	1555	1.9–4.0	7	1.8–4.5	63	2.2–14.2	13
Ephippididae					1.7–8.7	81					5.8–7.5	14
Gobiidae	3.7–10.5	235	1.2–17.7	643	1.1–10.1	8386	1.4–8.6	487	1.4–20.3	1207	1.9–9.0	258
Labridae	5.1–8.8	48	1.5–13.1	47	1.6–6.0	876	1.7–5.9	21	2.0–5.3	27	2.2–4.1	9
Lethrinidae	8.4–16.6	45	1.9–18.0	24	1.8–4.7	380	2.6–3.3	3	1.9–4.4	17	2.6–11.3	9
Lutjanidae			2.1–5.2	76	1.8–6.6	2740	2.1–7.4	33	1.8–4.9	105	2.5–8.4	48
Microdesmidae			1.5–4.8	10	2.0–4.3	100	2.2–3.2	9	3.3–5.4	6	2.9–6.3	7
Monacanthidae	46.6	1	1.5–23.3	13	1.2–4.6	608	1.9–3.3	3	1.8–3.7	11	2.0–6.3	22
Mullidae	11.2–21.9	51	21.5–39.7	54	2.4–4.9	8	5.1–23.6	2	22.4–30.2	10		
Nemipteridae	6.4–9.3	28	1.8–12.3	42	1.5–5.6	1548	1.8–5.2	15	1.6–5.0	75	4.2–4.8	4
Pinguepididae	2.0	1	1.4–6.5	30	1.3–5.6	2838	1.4–4.6	20	1.7–5.5	109	2.3–4.8	9
Platycephalidae			2.1–3.1	6	1.6–8.3	469	2.8–5.5	6	2.4–4.2	3		
Pomacentridae	5.3–14.9	7124	1.8–25.1	1248	1.0–14.6	496	1.9–9.4	22	1.8–11.7	30	6.4–14.6	68
Scaridae			1.6–4.4	30	1.7–4.6	136	2.2–4.0	34	2.5–7.7	10		
Schindleriidae					2.0–16.2	219	3.1–8.3	8	4.1–10.7	25	4.4–17.7	79

the larger individuals of most families. Analysis of the catch by method (Tables 1,2) suggests that the apparent selectivity of the light-trap reflects size-specific rather than taxonomic biases. The absence of certain taxa from the light-trap during the sampling period may mean that few large individuals were in the sampling area. Table 3 shows that, with the exception of bothids, schindleriids and carangids, taxa not caught by the light-trap were represented by relatively small individuals in the catch by other methods. Whether large carangids were present in more than trivial numbers is unclear. A single 57.4 mm carangid was taken by the light-seine, but the next-largest carangid taken by other methods was 14.2mm. The question of selectivity by light-traps must be resolved by more comprehensive sampling.

The light-seine and Tucker trawls captured most of the abundant families in all sizes. The neuston net and purse-seine captured the same abundant taxa, with size-ranges similar to one another. The exceptions were mullids, microdesmids, gobiids, and atherinids, for which the neuston net captured larger individuals. For the mullids and microdesmids, size distributions produced by the two methods overlapped slightly.

Catches by all methods were dominated by a few abundant families of fishes. The first five most-abundant families listed in Table 2 accounted for 80% or more of the catch by all methods. The Tucker trawl was the most equitable in terms of abundance distributions, and the light-trap the least. However, the rank order of abundant families was not the same for all methods (Fig. 2). The dominant families for all towed nets and the purse-seine were gobiids and apogonids. For light-trap and light-seine the dominant families were pomacentrids, followed by gobiids. Small apogonids, although consistently abundant in net samples, were not captured by light-aggregation devices. In light-trap catches, a single family—the Pomacentridae—accounted for 93% of individuals collected.

For most collecting methods, there was a high degree of consistency among samples. Results of PCA (Fig. 3) showed that samples taken by light-trap were

Table 3

Comparison of maximum size of the 19 abundant taxa (Table 2). Maximum size captured by light-trap is compared with maximum size captured by five other methods tested on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Taxa listed in increasing order of maximum size captured by 'other methods' (maximum size captured by the next-best 'other method').

	Maximum size (mm) captured by	
Taxon	Light-trap	Other methods
Callionymidae	not caught	4.9(4.5)
Microdesmidae	not caught	6.3(5.4)
Pinguepididae	2.0	6.5(5.6)
Scaridae	not caught	7.7(4.6)
Platycephalidae	not caught	8.3(5.5)
Lutjanidae	not caught	8.4(7.4)
Ephippididae	not caught	8.7(7.5)
Bothidae	not caught	10.0(7.7)
Nemipteridae	9.3	12.3(5.6)
Labridae	8.8	13.1(6.0)
Apogonidae	9.3	15.5(9.8)
Schindleriidae	not caught	17.7(16.2)
Lethrinidae	16.6	18.0(11.3)
Gobiidae	10.5	20.3(17.7)
Monacanthidae	46.6	23.3(6.3)
Pomacentridae	14.9	25.1(14.6)
Mullidae	21.9	39.7(30.2)
Carangidae	not caught	57.4(14.2)
Atherinidae	19.1	61.7(56.3)

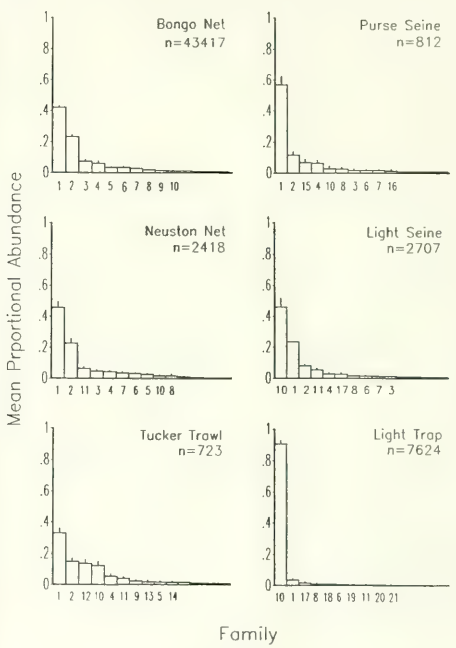

Figure 2

Mean proportional abundance (±1 SE, vertical axis, shown only upward) and ranked taxonomic categories of fishes (clupeoids excluded) collected by six sampling methods off Lizard Island, Great Barrier Reef on 3, 5, and 6 December 1986. Other sample data are given in Table 1. Key to taxa: **1** Gobiidae, **2** Apogonidae, **3** Pinguepididae, **4** Lutjanidae, **5** Carangidae, **6** Nemipteridae, **7** Callionymidae, **8** Labridae, **9** Monocanthidae, **10** Pomacentridae, **11** Atherinidae, **12** Schindleriidae, **13** Ephippididae, **14** Bothidae, **15** Scaridae, **16** Microdesmidae, **17** Mullidae, **18** Lethrinidae, **19** Synodontidae, **20** Scombridae, **21** Blenniidae.

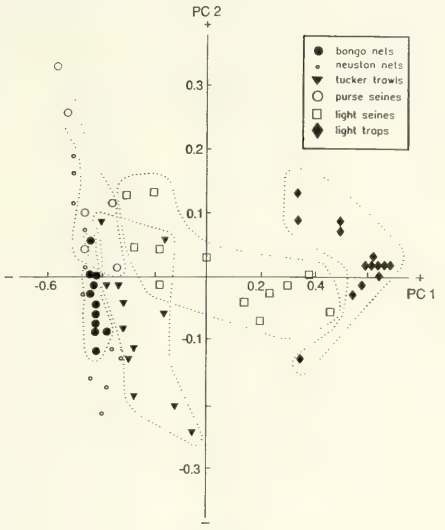

Figure 3

Results of Principal Components Analysis on proportional abundances of 19 families of fishes collected by six sampling methods on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Principal Components 1 and 2 are plotted. Differences between number of replicate samples and number of symbols for each method are due to overlap of some symbols.

distinct from net samples, and that samples taken by light-seine were intermediate between net and light-trap samples. Tucker trawl samples were almost completely distinct from bongo, neuston, and seine net samples. Bongo net samples formed a more discrete group than did the neuston and seine net samples.

The data sets for size analysis were heterogenous. Therefore, we attempted only to test for differences in density among methods within selected size-classes using single-factor ANOVA (df 3,39; $p<0.05$). The power of these tests to detect differences among methods was low. For apogonids, gobiids, lutjanids, and pomacentrids, there were sufficient numbers for statistical comparisons across the first three size-classes (i.e., <6 mm, Fig. 4). For all four families, density estimates provided by the bongo net were as high as, and in many cases higher than, those provided by the other nets. The Tucker trawl provided the lowest density estimates.

For the larger sizes (>6 mm), low or zero catches in some size-classes precluded statistical tests in most cases. We compared the Tucker trawl, which is designed to capture such large stages with the bongo net. The few tests that were possible show that in no instance did the Tucker trawl provide higher density estimates than the Bongo net (Fig. 4).

Two taxa, pomacentrids and gobiids, were sufficiently abundant to allow for comparisons of density by 2 mm size-classes between the aggregation devices. For pomacentrids we tested the 7–15 mm size-classes. Light-traps caught significantly higher numbers of pomacentrids in the 7, 9, and 11 mm size-classes than the light-seines (Fig. 4B). The two aggregation devices provided similar estimates of numbers for the 13 and 15 mm size-classes (Fig. 4B). The difference in overall density for pomacentrids sampled by light-traps and light-seines is due to the greater number of pomacentrids in the 7, 9, and 11 mm size-classes in the light-trap catches. Pomacentrid larvae >14 mm were collected by the light-seine on one night only.

Although we did not statistically test the gobiid data, the light-seine appeared to collect greater numbers of smaller (<4 mm), and the light-trap greater numbers of larger (>8 mm), individuals (Fig. 4B). The light-seine collected few gobiids >6 mm and the light-trap almost no gobiids <6 mm. Sizes of apogonid and lutjanid fishes sampled by the light-seine were similar to those of the purse-seine (Fig. 4C). No lutjanids and only four apogonids were collected by the light-traps.

Results of pooled samples from three nights for eight taxa (Materials and methods) by the different nets (Fig. 5) reflect both entry of fish into nets and subsequent extrusion. Most of the fishes taken by all nets were small (Table 2, Fig. 4). Bongo nets consistently provided the highest estimates of density of small fishes, especially gobiids, apogonids, lutjanids, labrids, and lethrinids. This reflects both the low-avoidance and high-retention properties of this fine-mesh net. The purse-seine filtered only small volumes of water, but provided high estimates of density, especially for gobiids, apogonids, and lutjanids (Fig. 4). Extrusion is probably minimal, due to the passive mode of filtering and the very fine mesh of this seine. Neuston nets provided low estimates of density for all families except two that concentrate in the surface layer—atherinids and mullids (Leis 1991a). Density estimates from the Tucker trawl were low for all families, most probably due to the loss of smaller larvae through its large mesh. Both atherinids and mullids, which attained large size (Table 2), were also poorly represented in Tucker trawl catches, possibly because the Tucker trawl did not sample the neustonic habitat of these taxa.

For aggregation devices, we compared densities of the important families identified by PCA, excepting apogonids and lutjanids which were rare or absent from light-traps. Light-traps collect mainly large individuals, so the samples were subdivided by size

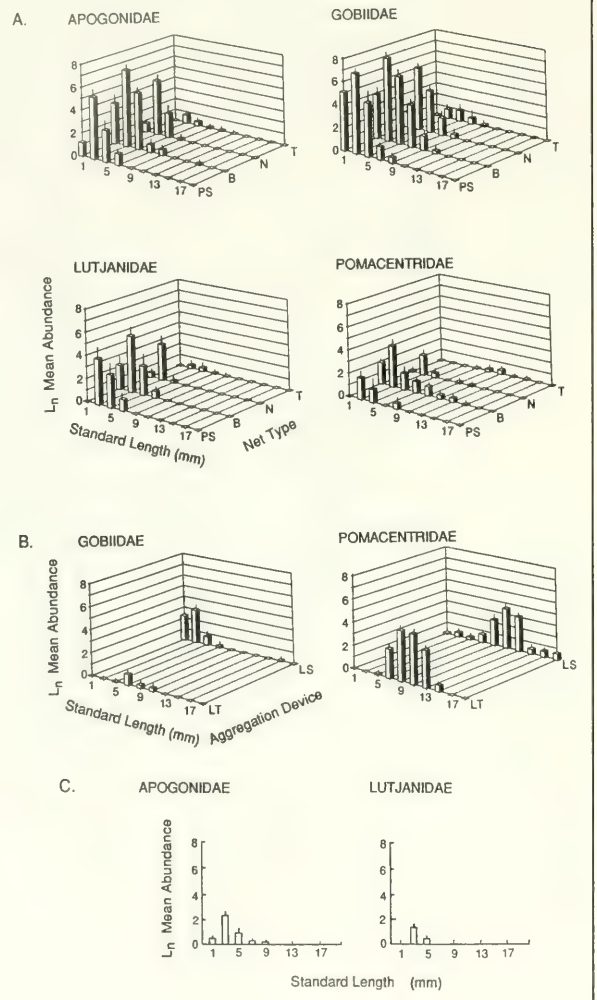

Figure 4

Analysis of size structure in selected families of fishes collected by six sampling methods on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. **(A)** L_n mean density/1000 m^3 (±SE) of four taxa in each of ten 2 mm size-classes collected by purse seine (PS), bongo net (B), neuston net (N), and Tucker trawl (T). **(B)** L_n mean density per sample (±SE) of gobiids and pomacentrids collected by light-trap (LT) and light-seine (LS). Size-classes as in (A). **(C)** L_n mean density per sample (±SE) of apogonids and lutjanids collected by light-seine. Size-classes as in (A).

(Table 4). Only three significant ($p<0.05$) differences were detected by *t*-tests. The light-trap caught greater numbers of large pomacentrids, the light-seine greater numbers of large atherinids and small gobiids.

Among-night variation

Larval and pelagic juvenile fishes may vary in density at a particular location over short time-periods ranging from hours to days. We examined the among-night variation in two contexts. First, we used factorial analysis to examine the variation attributable to method of sampling and sampling period (nights) in the net collections. Second, we examined the ability of nets and aggregation devices to detect trends in density of large individuals of some families over a longer time-period (five nights).

A multivariate factorial analysis of variance was used to examine trends in mean density in six families: apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids. Although both factors were significant (Table 5), the significant interaction between methods and nights (Pillai's Trace $F=1.65$; df 36, 186; $p<0.01$) indicates that differences among methods were not consistent over nights.

Canonical Discriminant Analysis was used to display the relationship between methods and night of sampling. Canonical variates 1 and 2 explained 93% of the variation in the data set (Table 6). Figure 6 illustrates the main conclusions from this analysis. Tucker trawls, and neuston and bongo nets each sampled a distinct fish fauna with little among-night variation. Purse-seine samples overlapped with those of the bongo nets on two nights and were the most variable, both within and among nights, probably reflecting the influence of few samples of small volume. Tucker trawl samples were characterized by consistently low numbers of the

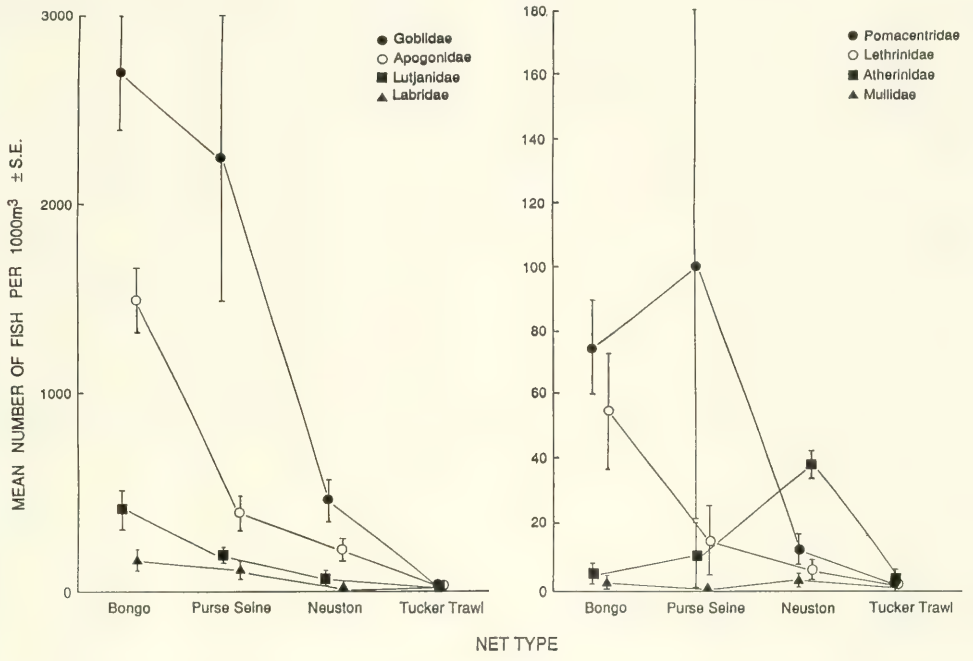

Figure 5

Mean densities of eight selected families (see Materials and methods) collected by four different net types on the nights of 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef.

Table 4

Density of six taxa of larval and juvenile fishes collected by aggregation devices on 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Data are mean densities (with 1SE) of fish per sample pooled over three sampling nights. Fish are divided into two size-classes: <6 mmSL (*S*mall) and >6 mmSL (*L*arge). * $0.05>p>0.01$; NS $p>0.05$.

Family	Size	Light-seine	Light-trap	p
Atherinidae	S	0.29± 0.22	0	
	L	9.36± 1.98	0.65± 0.25	*
Gobiidae	S	45.50±10.13	0.12± 0.08	*
	L	0.43± 0.23	8.92± 3.98	ns
Labridae	S	1.57± 0.62	0.04± 0.04	ns
	L	0.21± 0.11	1.54± 0.64	ns
Lethrinidae	S	0.43± 0.23	0	
	L	1.29± 0.34	1.38± 0.77	ns
Mullidae	S	0	0	
	L	3.86± 1.61	1.65± 0.68	ns
Pomacentridae	S	1.36± 0.52	0.27± 0.16	ns
	L	87.79 ±13.10	273.38±32.63	*

Table 5

Multivariate analysis of variance of density data for apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids (see Materials and methods) from off Lizard Island, Great Barrier Reef. Factors include sampling methods (purse-seine, bongo net, neuston net, Tucker trawl) and nights (3, 5, and 6 December 1986). Data are ln(x+1) transformed. Test statistic used is Pillai's trace. Significance levels: **$0.01>p>0.001$; ***$p<0.001$.

Source	F	Numerator df	Denominator df	p
Method	11.53	18	9	***
Night	4.05	12	54	***
Method×Night	1.65	36	186	**

dominant families; neuston, by higher numbers of atherinids, a neustonic group. The significant interaction is attributable largely to the purse-seine result.

Table 6

Standardized canonical coefficients from the Canonical Discriminant Analysis of density of fishes over each method by night combination, from samples taken off Lizard Island, Great Barrier Reef on 3, 5, and 6 December 1986. Data were ln(x+1) transformed.

Family	CAN 1	CAN 2
Apogonidae	5.031*	0.675
Atherinidae	–1.129	1.961*
Gobiidae	1.463	0.585
Lethrinidae	–1.005	–1.279
Mullidae	0.177	0.595
Pomacentridae	0.184	–0.736

Canonical variate	Proportion	Cumulative
1	0.793	0.793
2	0.134	0.927

* Consistently high values in total, between and within canonical structure. These variables contribute significantly to the discriminatory power of the canonical variate.

Data from all five nights provided more information on patterns of temporal change for some taxa (Fig. 7). We focused on the comparative ability of the different methods to detect changes over time in numbers of the larger (>6 mm) individuals of some families because we wished to know the best methods for identifying temporal pulses of large larvae and pelagic juveniles of reef fishes. Large pomacentrids and mullids serve as appropriate examples. Although absolute numbers of fishes taken by nets and aggregation devices could not be directly compared, temporal changes in patterns of density could be evaluated among these methods. Comparisons were made using all methods, although bongo net data were available for the nights of 3, 5, and 6 December only.

Data from the two aggregation devices indicated that large pomacentrids increased in density from the 2nd to a peak on the 5th, and decreased over the 6th and 7th (Fig. 7). This pattern was not present in the data from nets, each of which provided a different temporal pattern of density.

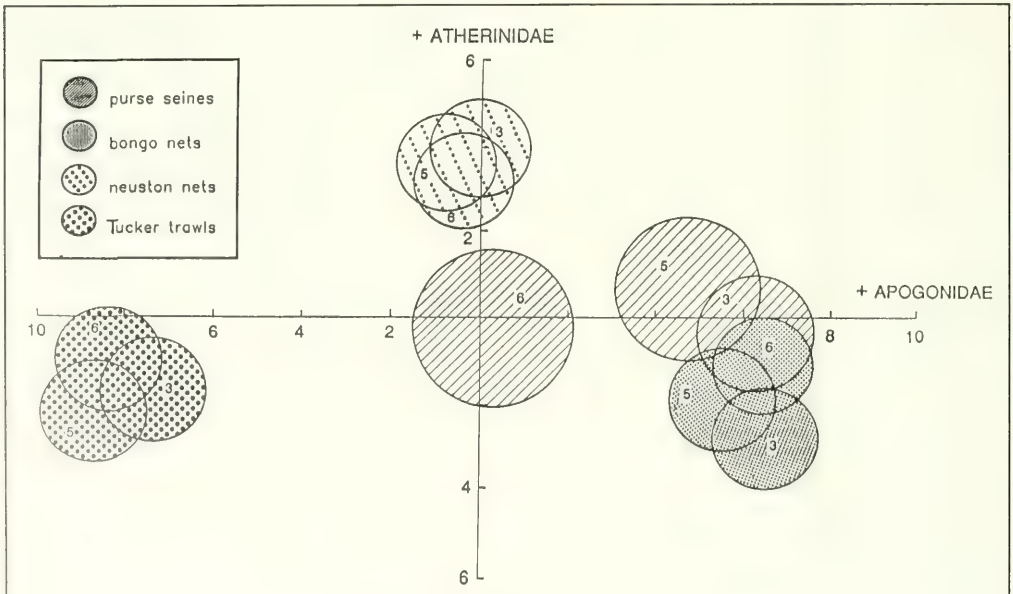

Figure 6

Results of Canonical Discriminant Analysis of density data (numbers/1000m^3) for apogonids, atherinids, gobiids, lethrinids, mullids, and pomacentrids taken by four net types on the nights of 3, 5, and 6 December 1986 off Lizard Island, Great Barrier Reef. Factors analyzed were net type and night of sampling. Canonical variates 1 and 2 are displayed. Numbers superimposed on circles refer to the day of sample.

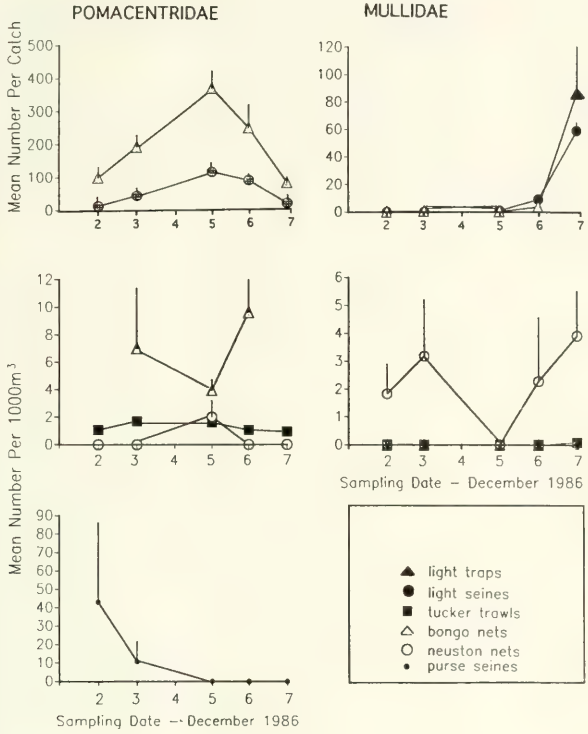

Figure 7

Changes in mean density (±SE) of large (>6 mm) pelagic pomacentrids and mullids sampled by six methods over six nights, 2–7 December 1986 off Lizard Island, Great Barrier Reef. Density estimates for the aggregation devices are not adjusted for volume sampled. Some methods did not collect large pomacentrids or mullids.

The aggregation devices indicated that large mullids were rare or absent until the 5th, and increased greatly in density on the 7th (Fig. 7). This trend was not present in data from the nets. Only the neuston net caught large mullids, but in low and variable numbers.

Discussion

The taxonomic composition obtained when sampling for larval and pelagic fishes is highly method-dependent. The bongo net captured the largest number of families, many of which were rare in the samples. Among abundant taxa, the four nets provided similar estimates of taxonomic composition. The light-trap, however, was more selective, and its catch differed in composition from that of the nets. Taxonomic composition of the light-seine samples was intermediate between the trap and nets, an expected result given its mode of operation.

Our results suggest that capture by the light-trap is dependent on fish size: larger pelagic stages are more likely to be attracted to the light and to swim into the trap than are small stages. However, trap performance may also be time-dependent. For example, apogonids, carangids, lutjanids, and scarids, which were rare or absent in light-trap catches during this study, have been captured during extended light-trap sampling around Lizard Island (M. Milicich, Griffith Univ., Nathan, Queensland, pers. commun.). The absence from light-traps at particular times may simply indicate that large or well-developed individuals of some families were not present at that time.

However, our study provides evidence that pelagic stages of some families may not be photopositive or enter traps, thus indicating some selectivity by the aggregation devices. Schindleriids were present in the net samples to adult size, yet were not captured with either of the light-aggregation methods. The net samples may have included the largest pelagic individuals of callionymids, and perhaps platycephalids and bothids, because they leave the pelagic environment (i.e., settle) at a relatively small size (see Table 3). These families were not present in the light-trap catches.

The size-distribution and density estimates of pelagic fishes captured also differ among nets. The bongo net, neuston net, and purse-seine captured predominantly smaller fishes. For abundant families, density estimates by the bongo net and purse-seine were generally similar, neuston net estimates were somewhat lower, and the Tucker trawl provided still lower estimates. The bongo net provided the highest abundance estimates for most sizes of most families. The Tucker trawl

undersampled smaller individuals, but was no better than the bongo net at capturing larger larvae and pelagic juveniles. This is consistent with the results of Kendall et al. (1987) and Clarke (1991), who compared bongo nets and larger trawls. The light-seine captured a wide size-range of fishes because it combined the sampling characteristics of both a purse-seine and an aggregation device.

Mesh size is an important determinant of catch composition because extrusion varies with mesh size. For a given mesh size, extrusion is a function of body shape and pressure across the net mesh (Clarke 1983 and 1991, Gartner et al. 1989). Body shape is species-specific, which emphasizes the importance of taxon-specific factors in methodological studies. Our results cover a comprehensive range of body shapes, from slender (gobiids) to deep bodied (apogonids and pomacentrids) to moderately deep with elongate fin spines (lutjanids), and should have general application. Purse-seines appear to herd planktonic organisms, while towed nets actively filter, often under considerable pressure; thus extrusion will vary between these two gear types regardless of mesh size. As our primary interest was in comparing a series of sampling devices in their normal working configuration, we did not attempt to test the effects of different mesh sizes within gear types.

Although vertical stratification is minimal at night in the study area (Leis 1986, 1991a), vertical distribution of the fishes could have affected apparent performance of the samplers because each method sampled somewhat differently in the vertical plane. Towed nets were deployed at fixed depths. Experience elsewhere has suggested that light-traps draw their catch from a relatively narrow depth stratum, the upper 5 m (P.J. Doherty, unpubl.). However, only in the neuston net can we confidently attribute greater catches (especially of atherinids) to vertical stratification. For this study, we assumed that vertical distribution of the fishes did not affect our evaluation of the other methods.

Horizontal or temporal variations in density may also have confounded comparisons. A position effect was possible because the aggregation devices were operated at fixed positions about 700 m apart (Fig.1). A temporal effect is possible because the bongo net and Tucker trawl tows were run in blocks and not randomized during each night's sampling, although the order of blocks was alternated among nights.

Absolute sampling efficiency of the nets was not measured. Our estimates of sampling performance were relative, because we did not obtain unbiased estimates of the true densities of small pelagic fishes. We did not attempt to use the methods of Somerton & Kobayashi (1989) to correct our net catches because we felt some of the assumptions required, especially those relating to patch size and consistency through time, were not appropriate in the case of our study. The smaller bongo net seemed to have equal or greater sampling efficiency than the larger Tucker trawl at night for large pomacentrids.

A comprehensive comparison of the six sampling methods would require two things. First, we would need to standardize all results as number of organisms per unit volume of water sampled. Second, we would require an estimate of the sampling precision of each device. For towed nets, both could be obtained because flowmeters provided estimates of the volume filtered for each tow. In the case of the purse-seine, it was not possible to obtain reliable estimates of the volume of water filtered during each deployment of the net. Minor variations in the deployment procedure can modify the dimensions of the volume enclosed by the net. At present, we have no reliable way of estimating this; therefore, for the purse-seine we have a general estimate of water filtered based on idealized dimensions of the deployed net.

Volumes sampled by aggregation devices cannot be estimated at this time, but preliminary calculations (below) suggest they may be large. The bongo net as operated in this study will sample ~4000 m^3/h, the Tucker trawl ~14,000 m^3/h, and we estimate the light-aggregation techniques could sample tens of thousands of m3/h. Therefore, light-aggregation techniques may be the best way to capture sufficient numbers of rarer, larger stages for useful analyses. Aggregation methods may offer considerable advantages in studies of settlement-stage reef fishes, but one must accommodate the characteristic taxonomic selectivity and unknown sample volume.

Two alternatives may explain the apparent disparity in numbers of larger pomacentrids estimated by the bongo net (average 6.9/1000 m^3; Tucker trawl catches averaged 1.49/1000 m^3) and the light-trap (average 273/h): (1) The bongo net undersamples these larger pelagic stages relative to the light-trap, or (2) the light-trap samples larger volumes of water. Assuming the two methods sample large pomacentrids with equal efficiency, the light-traps sample volumes on the order of 40,000m^3/h. This requires the trap to capture, with efficiency equal to that of the net, photopositive stages within a 7–50 m radius (to 5 m depth) of the trap, depending on the current speed (average in the area is 15 cm/s; Leis 1986) and geometry of the light field. It is not possible to choose between alternatives without a better measure of the effective volume swept by traps. Work in progress will help resolve this question.

Short-term temporal variation in the density of particular families was more obvious in the results of some methods than others. For the smaller size-classes, neuston, bongo, and Tucker nets gave consistent results

over short time-periods (Fig. 6). Catches from the purse-seine were more variable within a sampling period and showed greater variability among nights of sampling than did the towed nets. This reflects the localized sampling area and small sample volume of the purse-seine. For larger mullids and pomacentrids, similar trends in density over five nights were identified by the aggregation devices. These trends were not apparent in the data from the towed nets. Thus, the aggregation devices seem particularly suited to studies of short-term temporal variation in the larger (>6 mm) size-classes. The rapid and independent changes in density of the larger individuals of these two families suggest that larger pelagic stages are not present in the water at all times at a location. The alternative, that there are short-term taxon-specific changes in catchability due to changes in behavior of the fishes, seems less likely, but cannot be dismissed without further study.

A number of other studies have compared sampling methods for planktonic and pelagic assemblages. Purse-seines were found to be superior to towed nets for sampling larval anchovies (Murphy & Clutter 1972). Larger, faster, more-transparent nets may minimize net avoidance (Clutter & Anraku 1968). However, Smith & Richardson (1977) suggest that increased net size and towing speed may intensify the disturbance in front of the net and increase net avoidance. All towed nets in these cited studies employed towing bridles, which are a source of water disturbance and, thus, net avoidance by fishes. Towing bridles were not used in the present study, which may be why our conclusions differ from those of Clutter & Anraku (1968) and Murphy & Clutter (1972).

We agree, however, with Clarke (1991) who made detailed comparisons of the effectiveness of two types of bongo nets and a midwater trawl in capturing reef-fish larvae. He suggested that the bongo nets (0.7 m diameter with 0.183 mm mesh, and 1.25 m diameter with 2.5 mm mesh) sampled larvae as well or better than a 3 m Issacs-Kidd trawl (6 mm mesh). Clarke concluded that when densities of larvae were high, 0.7 m and 1.25 m bongo nets were the most effective methods for sampling small and large larvae, respectively. Although larger nets are assumed to capture more and larger fishes due to lessened avoidance (Clarke 1983 and 1991, Methot 1988), this was not true in our study nor is it always true in other pelagic groups (Barnes & Tranter 1965, Sands 1978, Pillar 1984).

One other significant study compared catches from a light-trap with those from a towed net. Gregory & Powles (1988) investigated a relatively simple planktonic assemblage of freshwater fishes. Based on a comparison of taxonomic composition and size of fishes, they concluded that both sampling methods should be used to avoid selectivity biases. An interesting conclusion that differs from our results was that the light-trap provided a better representation of size-classes, including smaller individuals, than did the towed net. This emphasizes the taxon-specific and, perhaps, habitat-specific nature of gear-performance measures.

We agree with Omori & Hamner (1982) that the sampling device and program selected must be question-driven (Kingsford 1988). In order to assist in the choice of appropriate methods, we summarize the performance and sampling properties of the six methods employed in this study (Table 7). Surveys of larval fishes are best accomplished with a bongo net. This will cover a significant portion of the size-range in many important taxa, including larger individuals, at least at night. No extra benefits were apparent from using the larger Tucker trawl. A major advantage of bongo nets is the relative ease with which they may be deployed and retrieved. As expected, neuston nets focused on neustonic fishes.

Surprisingly, the purse-seine provided results comparable to the bongo net despite the small volumes sampled. Among-sample variances were predictably

Table 7

Sampling characteristics of six methods used to collect planktonic and pelagic fishes at the Lizard Island study site, Great Barrier Reef.

Performance criterion	Bongo net	Neuston net	Tucker trawl	Purse seine	Light-trap	Light-seine
Size selectivity	Wide size-range; modal values at lower size.	Samples larger individuals of some taxa; modal values at lower size.	Samples larger sizes; no more effective than bongo net at night.	Primarily small individuals.	Primarily large individuals.	Wide size-range.
Taxonomic selectivity	Least-selective.	Neustonic taxa only.	Slender taxa and small individuals extruded.	Captures only shallow living taxa; undersamples rare taxa.	Selective; dependent on taxon behavior.	Combines light selectivity with characteristics of purse-seine.

higher than those of towed nets. Sampling of local-scale surface features requires the degree of spatial precision and replication provided by small purse-seines (Kingsford & Choat 1985 and 1986, Kingsford et al. 1991), but purse-seines cannot sample deeper than the upper few meters of the water column, and are difficult to operate in any but the best conditions. Localized replicated sampling may also be obtained by free-fall plankton nets (Kobayashi 1989) which, however, obscure vertical patterns and also have a small volume sampled.

Investigation of the patch size of pelagic organisms requires the ability to sample simultaneously over several spatial scales. Large-scale deployment of arrays of automated light-traps will increase replication and allow investigation of phenomena at several spatial scales without risk of temporal confounding, provided the traps can be retrieved over the same time-period. Also, both light-traps and purse-seining with aggregation devices may detect temporal pulses in the density of larger larvae and pelagic juveniles with greater reliability and precision than towed nets.

In addition to the sampling properties of the different devices, there are a number of more pragmatic considerations. Sorting and identification of samples may be a major bottleneck. This will be influenced by the size of the sample, the amount of organic material included, and condition of the fishes themselves. In this context, large samples taken by finer-mesh nets may be particularly difficult to process. Smaller or more selective samples are more readily processed, and those from purse-seines and light-traps yield living fishes suitable for rearing and experimentation. Further, the smaller the larva the more difficult it is to identify; thus, methods like the light-trap, which samples larger fishes, simplify identification.

It is clear that studies of the biology of small pelagic fishes require the use of both nets and aggregation devices either separately or in combination, depending on the type of question posed. No single method can provide a comprehensive picture of the larval and pelagic juvenile fish fauna, and few programs could cover the expense and logistic effort of the simultaneous deployment of a variety of methods. The picture one obtains of the larval and pelagic juvenile fish fauna is highly method-dependent. Which picture or combination of pictures is suitable for answering a given question varies with the question, the taxon, and the size-range of the fishes.

Acknowledgments

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Identification and distribution of *Urophycis* and *Phycis* (Pisces, Gadidae) larvae and pelagic juveniles in the U.S. Middle Atlantic Bight*

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Abstract.—Analysis of surface and subsurface plankton collections in the Middle Atlantic Bight (MAB) yielded larvae and juveniles of *Phycis chesteri* and five species of *Urophycis*. Identification was based on numbers of epibranchial gill rakers, abdominal vertebrae, and fin rays (dorsal, caudal, pelvic), patterns of pterygiophore interdigitation, and morphometric characters including body depth at the vent and a ratio between height of the pelvic-fin base and length of the mandible. *Urophycis tenuis* accounted for 99% of the *Urophycis* larvae and pelagic juveniles collected during spring off Virginia and New Jersey and was most abundant offshore. *Urophycis tenuis* larvae were smallest at offshore stations and increased in size as collections proceeded shoreward. *Urophycis chuss* was found in summer and fall collections off the coasts of New Jersey and Virginia, with abundances highest at midshelf stations. *Urophycis chuss* was the only species of hake found during August and early September, and it dominated summer ichthyoplankton collections. *Urophycis regia* was found primarily in midshelf areas off Virginia during fall, but was also collected offshore from both Virginia and New Jersey during winter. *Phycis chesteri*, also found in fall and winter collections, was restricted to offshore stations. Southern species, found exclusively in offshore winter collections, included *U. floridana* and *U. cirrata*.

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Species of the gadid genera *Urophycis* (Gill) and *Phycis* (Artedi), collectively referred to as 'hakes', are abundant on the continental shelf and slope of the northwest Atlantic Ocean. Six species of *Urophycis* and one species of *Phycis* are found in this area (Svetovidov 1948, Wenner 1983): *U. tenuis* (Mitchill), *U. chuss* (Walbaum), *U. regia* (Walbaum), *U. floridana* (Bean and Dresel), *U. earlli* (Bean), *U. cirrata* (Goode and Bean), and *P. chesteri* (Goode and Bean). Larval hake are present at all times of the year in the Middle Atlantic Bight (MAB) and dominate summer plankton collections (Comyns 1987), but persistent taxonomic problems (Dunn & Matarese 1984) have hindered the accumulation of ecological data on these important components of offshore ichthyoplankton communities (Kendall & Naplin 1981, Hermes 1985).

Newly hatched *U. chuss* and *U. regia* of known parentage were described by Hildebrand & Cable (1938), Miller & Marak (1959), Barans & Barans (1972), and Serebryakov (1978). Although these sources describe pigmentation differences between the two species, this information alone is insufficient to positively identify field-caught larvae.

Older larvae and juveniles of *U. chuss*, *U. regia*, *U. floridana*, and a single juvenile specimen of *U. earlli* were described by Hildebrand & Cable (1938). Larvae and juveniles of *U. regia* were collected off Beaufort NC and were identified by the presence of relatively few second dorsal-fin rays and lack of dark ventral-fin pigment. A second larval morph collected off Beaufort was tentatively identified as *U. floridana* because adult *U. floridana* was the only other species of *Urophycis* commonly found in the collection area. These specimens differed from *U. regia* in having darkly-pigmented ventral fins and more second dorsal-fin rays. A single juvenile specimen (37 mm) collected off Beaufort was identified as *U. earlli* because this specimen was darker than *U. regia* and *U. floridana*, and possessed smaller scales. Specimens of a fourth morph, collected off Cape Henry VA were identified as *U. chuss* because they possessed dark ventral-fin pigment, were relatively slender-bodied, and it was assumed that

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U. floridana would not be found as far north as Cape Henry.

Methven (1985) presented a size-dependent key to the identification of young *U. chuss*, *U. tenuis*, and *P. chesteri* from the Northwest Atlantic. Identifications were based on body depth, numbers of epibranchial gill rakers (Musick 1973, Wenner 1983), and numbers of caudal-fin rays. Material for Methven's study came primarily from Canadian waters, and he did not encounter *U. cirrata*, *U. earlli*, *U. floridana*, or *U. regia*. As a result, Methven's key is of limited use in more southerly locations where these species occur.

The objective of this paper is to describe additional morphometric and meristic characters that aid in the identification of *Urophycis* and *Phycis* larvae, and to describe the spatial and temporal distribution of these larvae collected 1975–77 off Virginia and New Jersey in the Middle Atlantic Bight.

Materials and methods

Sampling locations and shipboard procedures

Sampling extended from October 1975 until August 1977 and was conducted quarterly at 12 stations off Virginia and New Jersey (Fig. 1, Table 1). Neuston samples were collected with a floating sampler developed at Woods Hole Oceanographic Institution (Bartlett & Haedrich 1968, Craddock 1969). The net, constructed with 505 µm mesh Nitex, was 1 m wide and fished to a depth of 12 cm in calm seas. Tows were of 20 min duration at a ship speed of ~2 kn. The net was deployed from a boom and the towing course followed a widely-circular track to prevent sampling in the ship's wake. A single neuston tow was made at 3 h intervals over a 24 h period at each station, resulting in eight samples per station during each cruise. Two oblique tows between nearsurface and bottom were made at all stations with 60 cm opening-closing bongo systems (McGowan & Brown 1966), the first with paired 202 µm Nitex nets and the second with paired 505 µm nets. To prevent surface contamination, all nets were closed during passage through the surface layer (upper meter). Both bongo and neuston nets were equipped with flowmeters (General Oceanics, Inc.). The flowmeter attached to the underside of the neuston frame provided an estimate of horizontal distance relative to sea surface fished by the net. Estimates of volume filtered by the neuston sampler were determined by multiplying distance fished by net area fished (1 m×12 cm). In calm seas the neuston sampler consistently fished to a depth of 12 cm, but in rough seas the net opening would occasionally be almost completely filled or empty (the flowmeter was always submerged). This variability decreased precision of neuston volume estimates but was not expected to bias volume estimates. Comparisons between neuston and bongo collections were performed only to emphasize the relative importance of the surface layer to larval hakes. Patterns of the spatial and temporal distribution of larvae were based only on comparisons among neuston collections because most specimens were collected with this gear type.

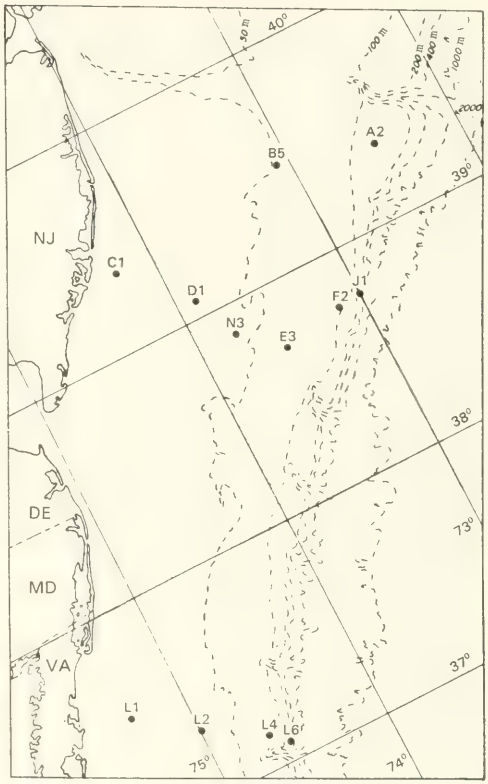

Figure 1
Ichthyoplankton sampling locations off New Jersey and Virginia. Stns. F2, J1, A2, L4, and L6 are considered offshore stations.

Laboratory procedures

Fish larvae were sorted from whole collections. All specimens of *Urophycis* and *Phycis* were cleared and stained (Dingerkus & Uhler 1977, Potthoff 1984, Tay-

Table 1

Sampling schedule for twelve stations occupied off New Jersey (NJ) and Virginia (VA), 1975–77.

	1975	1976				1977		
Stn.	Oct	Feb	Jun	Aug Sep	Nov	Feb Mar	May	Aug
C1 (NJ)	X	X	X	X	X	X	X	X
D1	X	X	X	X	X	X	X	X
N3	X	X	X	X	X	X	X	X
E3	X	X	X	X	X	X	X	X
F2	X	X	X	X	X	X	X	X
J1	X	X	X	X	X	X	X	X
B5 (NJ)					X	X	X	X
A2					X	X	X	X
L1 (VA)					X	X	X	X
L2					X	X	X	X
L4					X	X	X	X
L6					X	X	X	X

lor & Van Dyke 1985), except those occurring in collections taken during August–September 1976 (n>16,000) and August 1977 (n>4000). During these periods of high abundance, subsamples of over 2000 larvae from August–September 1976 and >900 larvae from August 1977 were randomly selected and similarly processed. Herein specimens <18 mmSL are arbitrarily termed larvae, whereas fish ≥18 mm are termed juveniles (Markle et al. 1982). Fish <~12 mm were measured with an ocular micrometer, while lengths of larger specimens were measured with a dial caliper ruler. The largest pelagic juveniles found were ~40 mmSL.

The following morphometric criteria were used in the analysis: (1) height of pelvic fin/vertical distance from base of pelvic fin to ventral margin of body; (2) mandible length/distance from anterior tip of the dentary to posteroventral tip of the angular; and (3) body depth at anus/vertical distance from anterior end of anal-fin base to dorsal surface immediately above. Morphometric measurements were made with an ocular micrometer. The first interneural space was defined as the space anterior to the first neural spine.

Hake larvae and juveniles possessing the adult meristic complement were initially identified using published and unpublished meristic data (Table 2). Meristic observations included epibranchial gill rakers (left side examined), abdominal vertebrae, and fin rays (dorsal, caudal, pelvic). Observations were taken from both cleared and stained material and from radiographs of juvenile and adult museum specimens (App. Table 1).

Identification of smaller larvae was facilitated by using morphometric criteria, patterns of interdigitation between pterygiophores supporting the median fins and the neural or haemal spines, and by defining the size at which larvae attained various stages of fin-ray, vertebral, and gill-raker development. Unfortunately, faded pigmentation caused by specimen storage in formalin and subsequent clearing and staining prevented use and further description of larval pigmentation in the present study.

Table 2

Ranges of meristic characters in *Phycis chesteri* and six species of *Urophycis*. Numbers in parentheses indicate meristic ranges that were extended by the present study. Data sources are (1) Svetovidov 1948, (2) Hildebrand & Cable 1938, (3) Bigelow & Schroeder 1953, (4) Leim & Scott 1966, (5) Miller & Jorgenson 1973, (6) Musick 1973, (7) Hoese & Moore 1977, (8) Markle 1982, (9) Fahay 1983, (10) Wenner 1983, (11) Methven 1985, (12) J.A. Musick, pers. commun., VIMS, Gloucester Point VA 23062.

	U. tenuis	*U. chuss*	*U. regia*	*U. floridana*	*U. earlli*	*U. cirrata*	*P. chesteri*
Caudal-fin rays	33–38(40)	28–34	28–32(34)	28–32(34)	27–30(31)	28–33	28–35(36)
1st dorsal-fin rays	9–10(12)	9–11(12)	8–10	10–13	8–11	9–11(12)	8–11(12)
2nd dorsal-fin rays	50–59(62)	(52)53–64	43–51(52)	54–63	57–63(68)	54–68	50–63
Anal-fin rays	41–52(53)	45–57	41–50(52)	45–54(55)	49–56(60)	46–58	43–54
Vertebrae (total)	47–50(51)	45–50(51)	(44)45–47(48)	44–50(51)	45–47(48)	47–53	45–52
Caudal vertebrae	(32)34–35	33–36	(30)31–33(34)	30–34(35)	31–33(34)	32–37	31–37
Abdominal vertebrae	13–17	14–17	13–15	14–17	14–15	15–17	13–16
Pelvic-fin rays[b]	3	3	3	3	3	3	3
Epibranchial gill Rakers (1st arch)	2	3	3	2	2	3	4–5
Data source	1,3,6,8,11	1,2,4,5,6,8,11	1,2,3,4,5,8	1,7,12	1,5,12	1,12	1,10,11,12

In our material (n=205) *U. tenuis* never possessed <15 abdominal vertebrae.
[b] The third pelvic-fin ray in adult *Urophycis* and *Phycis* is rudimentary.
[c] *Urophycis tenuis* occasionally has three epibranchial gill rakers.

Results

Identification of *Urophycis* and *Phycis* larvae and juveniles

Meristics

Epibranchial gill rakers (Table 3) A complete size-series of all species was not available, but size (mm) at which *U. regia*, *U. chuss*, and *U. tenuis* larvae attain the adult complement of epibranchial gill rakers and other meristic elements is shown in App. Table 2. The following sections are abbreviated to avoid repeating in the text what the tables and figures succinctly show. *Phycis chesteri* does not attain the adult complement of epibranchial gill rakers until 16–18 mm (Methven 1985), but by 13 mm the third gill raker has developed and serves to separate larvae of this species from *U. tenuis*, *U. earlli*, and *U. floridana*. Occasionally *U. chuss* and *U. regia* possess two or four epibranchial gill rakers on one side, but most of these specimens have the normal complement of three gill rakers on the other side. *Urophycis tenuis* occasionally possesses a 3rd epibranchial gill raker, but only very rarely is this third gill raker found on both sides of a specimen.

Caudal-fin rays (Table 3) All but two specimens of *U. tenuis* (n=195) had more caudal-fin rays than all other species of *Urophycis*. Numbers of caudal-fin rays of *U. tenuis* overlapped those of *P. chesteri*, but more than half of our *U. tenuis* were distinct in having >36 rays, and over 40% of *P. chesteri* (n=56) differed from *U. tenuis* in having <34 rays. As few as 28 caudal-fin rays have been reported in *P. chesteri* (Wenner 1983) and *U. cirrata* (J.A. Musick, VA Inst. Mar. Sci., pers. commun.), but this may be because some of the small procurrent rays are not easily seen in radiographs of larger fish.

No *U. earlli* specimens (n=31) possessed >31 caudal-fin rays, while all other hake commonly have >31 rays.

Dorsal-fin rays (Table 3) Despite overlapping extremes, numbers of first dorsal-fin rays helped distinguish *U. floridana* from other species of hake. In our material, *U. regia* and *U. earlli* never possessed >10 and 11 first dorsal-fin rays, respectively, while over 80% of *U. floridana* (n=45) had >11 rays. One-third of *U. floridana* specimens examined possessed 13 first dorsal-fin rays, delimiting these from all other hake taxa.

The relatively low number of second dorsal-fin rays in *U. regia* separated this species from *P. chesteri* and other *Urophycis* species with little overlap. *Urophycis chuss* and *U. regia* with incomplete development of second dorsal-fin rays were delimited by numbers of pterygiophores supporting these rays at sizes as small as 6 mm (Fig. 2). Although extremes in numbers of second dorsal-fin rays overlapped in all other taxa, many of the available specimens of *U. earlli* and *U. cirrata* were distinct in possessing >63 rays.

Abdominal vertebrae (Table 3) Numbers of abdominal vertebrae cannot be used alone to identify individual specimens because of overlapping extremes, but this meristic character is useful when identifying collections comprised entirely of *U. tenuis* or *U. chuss*. *Urophycis tenuis* larvae, identified by numbers of epibranchial gill rakers and caudal-fin rays, were found in the MAB only in spring and accounted for 99% of the *Urophycis* collected at this time (*U. regia* juveniles accounted for the other 1%). *Urophycis* larvae <10 mm (n=154) that were present in spring collections had not yet developed the adult complement of caudal-fin rays, but these larvae (>4 mm) had developed the adult complement of abdominal vertebrae and were identified as *U. tenuis* because their frequency-distribution of numbers of abdominal vertebrae was identical to that found in larger *U. tenuis*; 88% of the larvae had 16 abdominal vertebrae, and no specimens were found with <15. It is unlikely that any of these small larvae were *U. floridana* or *U. cirrata*, two other species with similar numbers of abdominal vertebrae, because these two southern species were found only in offshore winter collections and most specimens were pelagic juveniles.

Urophycis chuss >4 mm (n=448) possessed 14–16 abdominal vertebrae, but the majority of specimens (n=391) had 15. In all other species of *Urophycis* the count of 15 occurred in <20% of the specimens; and although extremes of *U. chuss* and *P. chesteri* were similar, *P. chesteri* commonly had 14 or 16 abdominal vertebrae (17%). Consequently, in the MAB during late summer when *U. chuss* larvae are extremely abundant (and, in this study, were the only species of hake found at this time), complete meristic counts to check for species other than *U. chuss* need be performed only on those specimens that do not have 15 abdominal vertebrae. If species other than *U. chuss* are found in late-summer collections, numbers of abdominal vertebrae are no longer taxonomically useful and complete meristic counts are necessary to identify larvae.

Urophycis regia (n=698) had 13–15 abdominal vertebrae, but only eight specimens had 15, and seven of these specimens had an anomalous 15th abdominal vertebra. This anomalous vertebra possessed one short transverse process characteristic of abdominal vertebrae and one long transverse process typical of caudal vertebrae. Because 99.9% of *U. regia* examined had <15 normal abdominal vertebrae, it was assumed that specimens with ≥15 abdominal vertebrae were not *U. regia*. This meristic character aided in the separation of small (<6 mm) *U. chuss* and *U. regia* in fall collec-

Table 3

Frequency distribution of meristic values recorded in *Phycis chesteri* and six species of *Urophycis*. Asterisks denote that data from juvenile and adult specimens are included. All larvae had attained the adult meristic complement.

Epibranchial gill rakers on left first gill arch. Slash separates numbers on left and right sides.

	2	3/2	3	4/3	4	5
P. chesteri					24	8
U. chuss		8	596	8	2	
U. regia		4	631	4	2	
U. cirrata			19			
U. tenuis	160	6	1			
U. floridana	44					
U. earlli	32					

Number of caudal-fin rays

	29	30	31	32	33	34	35	36	37	38	39	40
U. tenuis						2	28	56	65	34	9	1
P. chesteri			1	8	15	19	10	3				
U. regia		1	19	34	16	1						
U. chuss	1	1	22	13	10	3						
U. cirrata			3	8	2							
U. floridana		5	13	21	14	2						
U. earlli	12	13	6									

Number of first dorsal-fin rays

	8	9	10	11	12	13
U. floridana				8	22	15
U. cirrata			2	8	3	
U. chuss		2	33	51	9	
U. tenuis		10	24	26	3	
P. chesteri	1	19	38	13	2	
U. earlli		6	21	5		
U. regia	14	61	7			

Number of second dorsal-fin rays

	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
U. cirrata																1		1	1	1	2	2	5		1
U. earlli														1			2	8	8	3	7	1	1		1
U. floridana												6	6	7	9	6	5	3	3						
P. chesteri										3	8	5	14	13	5	5	3	1		1					
U. chuss									1	3	4	6	16	16	16	20	9	6	6	3					
U. tenuis								1	3	9	7	8	3	12	5	4	1	1	2						
U. regia	2	1	15	22	30	36	29	16	2																

Number of abdominal vertebrae

	13	14	15	16	17
U. tenuis			20	180	5
U. cirrata			2	10	1
U. floridana		1	7	38	3
U. chuss		50	391	7	
P. chesteri		8	57	4	
U. earlli		27	4		
U. regia	66	624	8		

Note: Although 8 specimens of *U. regia* had 15 abdominal vertebrae, in only one of these specimens (0.1%) was the 15th vertebra normally developed.

Number of anal-fin pterygiophores anterior to first haemal spine

	3	4	5	6	7	8	9
U. earlli				4	14	8	1
U. floridana				11	23	7	1
U. regia			8	156	202	14	
U. chuss			18	173	152	7	
U. tenuis		3	36	25	1		
U. cirrata		1	8	2			
P. chesteri	3	28	34	5			

Interneural space into which projects the pterygiophore supporting the first ray of the second dorsal fin

	7	8	9	10
U. tenuis		8	52	6
U. floridana	1	10	25	6
P. chesteri	3	31	20	1
U. chuss	1	203	220	4
U. regia	141	41		
U. earlli	15	12		

Note: If pterygiophore was aligned with the tip of a neural spine, it was arbitrarily recorded as pointing into the space posterior to the spine in question.

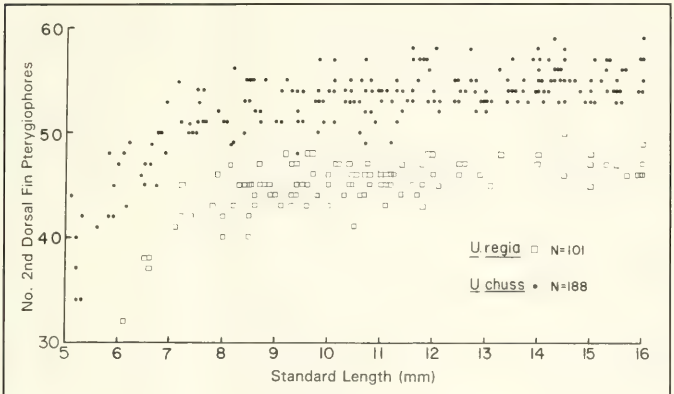

Figure 2
Development of second dorsal-fin pterygiophore number in *Urophycis chuss* and *U. regia*.

tions when numbers of second dorsal-fin pterygiophores were not yet taxonomically useful.

Numbers of abdominal vertebrae may help separate *U. earlli* from *U. floridana* and *U. cirrata*, the other two southern species of *Urophycis*. Over 80% of *U. floridana* and *U. cirrata* possessed 16 or 17 abdominal vertebrae, but *U. earlli* has never been recorded with this many.

Anal-fin pterygiophores (Table 3) The number of anal-fin pterygiophores positioned anterior to the first haemal spine helps distinguish *P. chesteri*, *U. cirrata*, and *U. tenuis* from *U. earlli*, *U. floridana*, *U. regia*, and *U. chuss*. Only one specimen of *U. tenuis* (n=65) and no *U. cirrata* (n=11) or *P. chesteri* (n=70) were found with >7 anal-fin pterygiophores positioned anterior to the first haemal spine, but 45% of *U. chuss* (n=350) and over half of *U. earlli* (n=27), *U. floridana* (n=42), and *U. regia* (n=380) had at least 7 of these pterygiophores. More than 60% of *U. tenuis*, *U. cirrata*, and *P. chesteri* had <6 anterior anal-fin pterygiophores, whereas <2% of *U. regia* and no *U. earlli* or *U. floridana* had this few.

Second dorsal-fin pterygiophores (Table 3) The interneural space into which points the first pterygiophore of the second dorsal fin helped separate *U. chuss* from *U. regia*, and *U. floridana* from *U. earlli*. In over half of *U. chuss* examined (n=431) the first pterygiophore of the second dorsal fin pointed into the 9th or 10th interneural space, whereas in all *U. regia* examined (n=182) this pterygiophore pointed into the 7th or 8th interneural space. In >75% of *U. regia* this pterygiophore pointed into the 7th interneural space, whereas <1% of *U. chuss* showed this pattern.

In >70% of *U. floridana* examined (n=42) the first pterygiophore of the second dorsal fin pointed into the 9th or 10th interneural space, whereas in all juvenile and adult *U. earlli* examined (n=27) this pterygiophore pointed into the 7th or 8th interneural space. In over half of *U. earlli* examined, the first pterygiophore of the second dorsal fin pointed into the 7th interneural space, but in only 2% of *U. floridana* did this pterygiophore project this far forward.

Morphometrics

Body depth at anus (Fig. 3) Body depth at the anus separated some species of hake larvae at sizes >12–13 mm. Extremes of body depth as percent of standard length for cleared and stained *P. chesteri*, *U. tenuis*, and *U. chuss* were 21.0–23.4, 19.0–21.1,

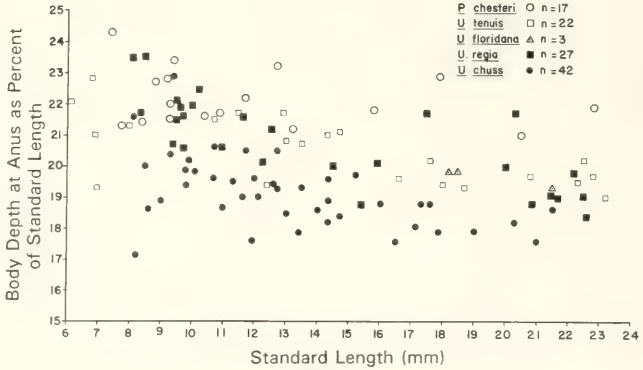

Figure 3
Body depth at anus as a percent of standard length plotted against standard length for larvae and juveniles of *Phycis chesteri* and four species of *Urophycis*.

Table 4

Ranges of pelvic-fin-base height as percent of mandible length for *Physis chesteri* and five species of *Urophycis*. Ranges of values are given for different size-intervals of larvae. ND = no data.

		Size-interval (mm)						
		5–9	10–14	15–19	20–24	25–29	30–34	35–45
U. regia	(*n*=31)	21–30	19–33	19–25	16–28	12–17	ND	ND
U. floridana	(*n*=19)	ND	ND	29–36	23–37	23–28	24–29	ND
U. chuss	(*n*=38)	20–39	23–33	24–36	19–22	15–16	16	16
U. cirrata	(*n*=4)	ND	ND	ND	39	31	ND	19–31
P. chesteri	(*n*=29)	44–74	52–61	54–61	46–61	52–64	50–59	26–57
U. tenuis	(*n*=39)	28–42	24–42	33–40	29–37	26–30	32	ND

and 17.6–19.7, respectively. Body depth of *U. floridana*, however, was found to overlap extremes of *U. tenuis* and *U. regia*, while *U. regia* exhibited the greatest variation in this character, overlapping the extremes of *P. chesteri* and all other species of *Urophycis* studied.

Mandible length and height of pelvic fin (Table 4, Fig. 4) Height of the pelvic fin plotted against mandible length separated larval *P. chesteri* from other hake at sizes between ~6 and 35 mm. At sizes > 3 5 m m *P. chesteri* was similar to *Urophycis* with respect to this character because *P. chesteri* became more slender-bodied and the pelvic-fin origin moved closer to the ventral margin of the body. Ranges of pelvic-fin height as percent of mandible length in cleared and stained larvae ranging in length from 6 to 35 mm varied from 44 to 74% in *P. chesteri* (*n*=29), but the highest value of this ratio in five species of *Urophycis* (*n*=131) was only 42%.

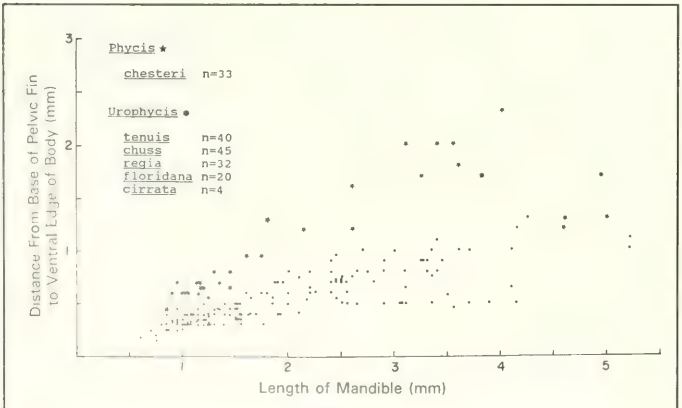

Figure 4

Height of the pelvic fin plotted against mandible length for larvae and juveniles of *Physis chesteri* and five species of *Urophycis*.

Distribution and abundance of hake larvae

Urophycis chuss *Urophycis chuss* was found only in summer and fall plankton collections from the MAB, and was the only species of larval hake found in August and early September. Densities of *U. chuss* in summer collections off the coast of New Jersey were up to two orders of magnitude greater than densities found off Virginia (Fig. 5). In October 1975 and November 1976, *U. chuss* were still present off both Virginia and New Jersey, but were far less abundant than during summer.

Densities of larval *U. chuss* also varied with distance from shore (Fig. 5), particularly during summer when lowest densities occurred inshore and highest densities were found in midshelf regions in water depths of 40–120 m. Variations in larval density with both latitude and water depth were not well defined in f a l l collections.

An increase in mean size of *U. chuss* was evident in fall collections (Fig. 6). As larval size increased in fall collections, the number of larvae collected with bongo nets decreased greatly. More than 1300 specimens were collected in October 1975 and November 1976, but only 25 of the larvae were collected with bongo gear. Onshore-offshore variation in size of *U. chuss* was most evident in fall collections off both Virginia and New Jersey; size tended to increase with decreasing water depth.

Urophycis regia *Urophycis regia* was collected in the MAB from October until May, with highest densities of larvae occurring in fall collections off the Vir-

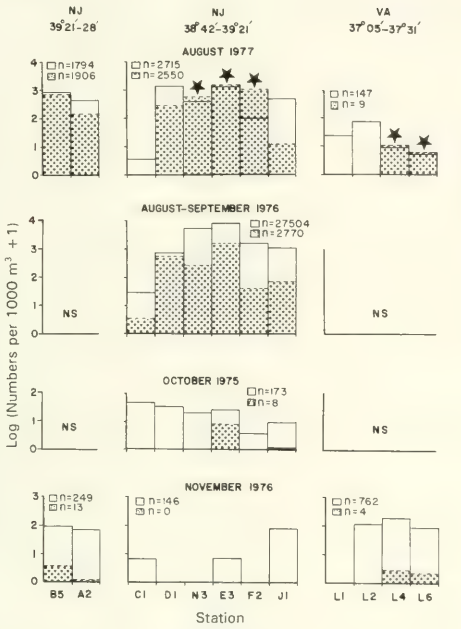

Figure 5

Mean abundance of *Urophycis chuss* in neuston and bongo collections at stations off Virginia and New Jersey, October 1975–August 1977. *n* = number of larvae collected. Neuston catches are denoted by clear histograms; bongo catches by stippled histograms. NS = no samples taken. Star denotes bongo catches exceed neuston catches.

ginia coast at midshelf station L2 (Fig. 7). Densities of *U. regia* were much lower in collections taken in February and March, and most specimens were pelagic juveniles found at offshore stations off both Virginia and New Jersey. By May, *U. regia* was scarce; only seven neustonic juveniles were found at offshore stations.

Urophycis tenuis Apart from an occasional *U. regia* juvenile found at offshore stations, *U. tenuis* was the only species of hake present in spring plankton collections off Virginia and New Jersey. Abundance of *U. tenuis* in May 1977 was up to one order of magnitude greater than abundances in June 1976 (Fig. 8). Larvae were collected at all but inshore stations off both Virginia and New Jersey, but were most abundant at offshore stations. Larvae were smallest at offshore stations and increased in size as collections proceeded inshore (Fig. 9, page 220).

Urophycis floridana and U. cirrata *Urophycis floridana* (*n*=41, 13–32 mmSL) and *U. cirrata* (*n*=5, 20–42 mmSL) were found exclusively in offshore winter collections (Fig. 10, page 221). With the exception of a single juvenile *U. floridana* (23.0 mmSL) captured in a bongo tow, all specimens were found in neuston samples.

Phycis chesteri *Phycis chesteri* larvae first appeared in fall neuston collections from the Middle Atlantic Bight; 16 larvae 6–13 mm in length were collected in November 1976 at offshore stations off Virginia (Fig. 11, page 221). *Phycis chesteri* larvae and pelagic juveniles remained in surface waters during winter and were found in water deeper than ~100 m off both Virginia and New Jersey (*n*=41). All specimens were collected with the neuston net.

Discussion

Because of similarities between larvae of the seven hake species found in the MAB, a dichotomous key is not a practical tool with which to identify hake larvae in this area. However, the specific identification of larval and pelagic juvenile hake is feasible using a suite of diagnostic characters (App. Table 2). Identifications in this study were based on comparison of larval meristics with adult meristics. Further examination of larvae revealed diagnostic characters comprised not only of meristic information, but also morphometric and pterygiophore interdigitation data. Spawning season and capture location were not used as 'characters' to identify larvae in this study.

Methven (1985) had limited success using pigment characters to separate *U. chuss* and *U. tenuis* >7–8 mm. Problems will persist with the identification of small hake larvae until ontogenetic pigment patterns of all species have been described. These ontogenetic pigment patterns, when used in concert with meristic characters, will hopefully enable relatively routine identifications of these taxa.

The only species of *Urophycis* not found in the present study was *U. earlli*. Adult *U. earlli* are rare and larvae remain undescribed, but they are expected to co-occur with *U. floridana* (Hildebrand & Cable 1938). Both species are similar in having two epibranchial gill rakers, but numbers of first dorsal-fin rays, abdominal vertebrae, and caudal-fin rays delimit most specimens of these two species.

Larval and juvenile *Urophycis* or *Phycis* were present in the MAB throughout the year, and patterns of spatial and temporal distribution of larvae were consistent during both years of this study. *Urophycis chuss* larvae were found in summer and fall collections, with greatest abundances occurring during summer in the

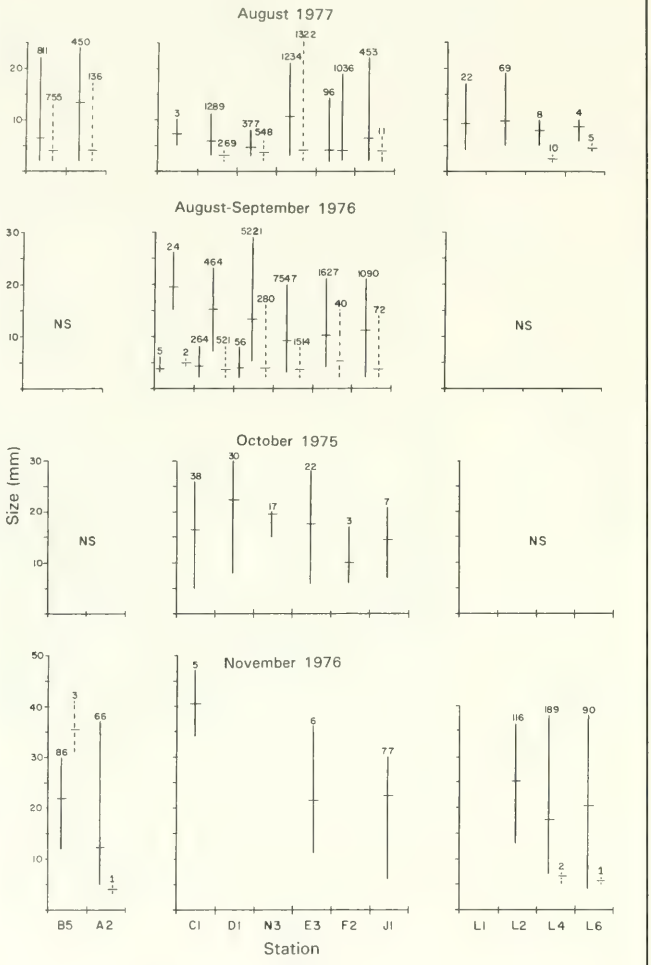

Figure 6

Range and mean size of *Urophycis chuss* in neuston and bongo collections at stations off Virginia and New Jersey. Solid and dashed lines indicate neuston and bongo collections, respectively. Horizontal lines show mean values. Two neuston ranges are shown if more than one size-mode is present. NS = no samples taken; numbers = no. larvae/1000m^3.

central and northern MAB where water depth was 40–60 m. *Urophycis chuss* was the only species of larval hake found in summer collections, and accounted for 80% of all hakes collected during this 2-year study.

Most *U. regia* in the present study were collected in November, but some larvae or neustonic juveniles were collected from October to May. *Urophycis regia* in the MAB is reported to spawn from late September through November, and possibly to February, with peak activity in October (Barans & Barans 1972). *Urophycis regia* was most abundant during fall in the southern MAB in the relatively shallow (41–43 m) midshelf area. Size range of *Urophycis regia* collected in this area was 2–34 mm, and although some of the larger specimens may have drifted from deeper water, small larvae were most likely spawned on the shallower central shelf. Evidence of *U. regia* spawning in shallow water was also found in October 1975 off New Jersey where larvae as small as 4mm were found in water as shallow as 12 m. However, not all specimens off New Jersey originated in shallow water; a second group of larvae 6–23 mm in length was found offshore.

The offshore distribution of *U. regia* became quite distinct in winter collections, with abundances being greatest at offshore stations in February 1976, February–March 1977, and May 1977. These *U. regia* were probably spawned in offshore waters of the MAB or in offshore waters of the South Atlantic Bight and transported northward. Larval *U. regia* have been found in abundance in winter collections from offshore waters off North Carolina in the South Atlantic Bight (Fahay 1975, Powles & Stender 1976).

Late-summer spawning by *U. tenuis* occurs in shallow water of the southern Gulf of St. Lawrence and the Scotian Shelf (Markle et al. 1982). Fahay & Able (1989) suggest the existence of a second stock of *U. tenuis* that spawns in deep water during early spring on the slope of Georges Bank, and probably also along the slopes of the Scotian Shelf, southern New England, and the MAB. The present study found direct evidence of spring spawn-

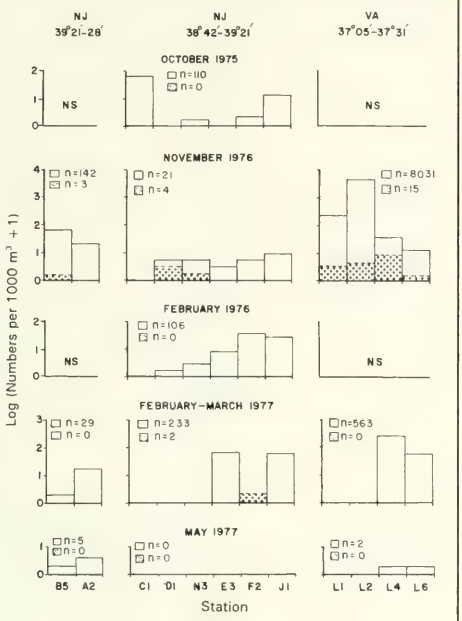

Figure 7

Mean abundance of *Urophycis regia* in neuston and bongo collections at stations off Virginia and New Jersey, October 1975–May 1977. *n* = actual number of larvae collected. Neuston catches denoted by clear histograms, bongo catches denoted by stippled histograms. NS = no samples taken.

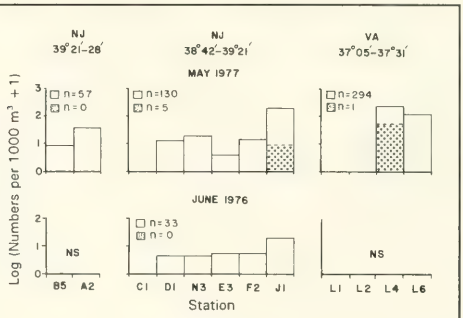

Figure 8

Mean abundance of *Urophycis tenuis* in neuston and bongo collections at stations off Virginia and New Jersey, June 1976 and May 1977. *n* = actual number of larvae collected. Neuston catches denoted by clear histograms, bongo catches denoted by stippled histograms. NS = no samples taken.

ing by *U. tenuis* in deep water of the MAB; in May 1977 *U. tenuis* larvae as small as 3–4 mm were found over the continental break and slope off both New Jersey and Virginia. In June 1976 *U. tenuis* found at offshore stations were 16–38 mm in length. Based on estimated larval and pelagic juvenile growth rates of 10–22 mm/mo (Markle et al. 1982) and demersal juvenile growth rates of ≈30 mm/mo (Fahay & Able 1989), these fish were probably spawned in late April and May.

Fahay & Able (1989), studying young *U. tenuis* in the Georges Bank area, found a shoreward migration with growth. Recruitment to nearshore areas was also indicated in the present study by the increasing size of *U. tenuis* as collections proceeded shoreward. Neustonic juveniles (35–53 mm) were captured in water as shallow as 32 m off the coast of New Jersey.

Urophycis floridana and *U. cirrata*, two southern species of hake, were found off New Jersey and Virginia only in offshore winter collections. The large size and offshore distribution observed for both species suggest that these pelagic juveniles may have been transported northward into the study area. Larvae of *U. earlli*, another species found south of the MAB, are rare and remain undescribed, but this species may also occur occasionally in offshore waters of the MAB during winter. Hildebrand & Cable (1938) expected *U. earlli* to be a winter spawner after collecting three juveniles (37, 75, 103 mm) in March and April off North Carolina, and Fahay (1975) collected a few neustonic *U. earlli* in winter in the South Atlantic Bight.

Phycis chesteri larvae and pelagic juveniles appeared at offshore stations in fall and winter off Virginia and New Jersey. This larval distribution concurs with Wenner (1983) who found adult *P. chesteri* generally at depths >183 m on the continental slope from 36°N to 47°N in the western North Atlantic, and noted that spawning off Virginia took place between late September and April, with peak spawning occurring in December and January. Methven & McKelvie (1986) collected 51 *P. chesteri* larvae and pelagic juveniles along the edge of the continental shelf in the MAB, Grand Bank, and Labrador Shelf, and based on estimated growth rates suggested that most spawning occurs in October.

This study has shown the spatial and temporal distribution of hake larvae in the MAB to be more complex than previously thought. Additional taxonomic characters, particularly ontogenetic pigment patterns, are still needed in order to routinely identify small hake larvae, and more research is needed to explain the observed patterns of larval distribution. Of particular interest is an understanding of the processes that result in the northward transport of larvae and

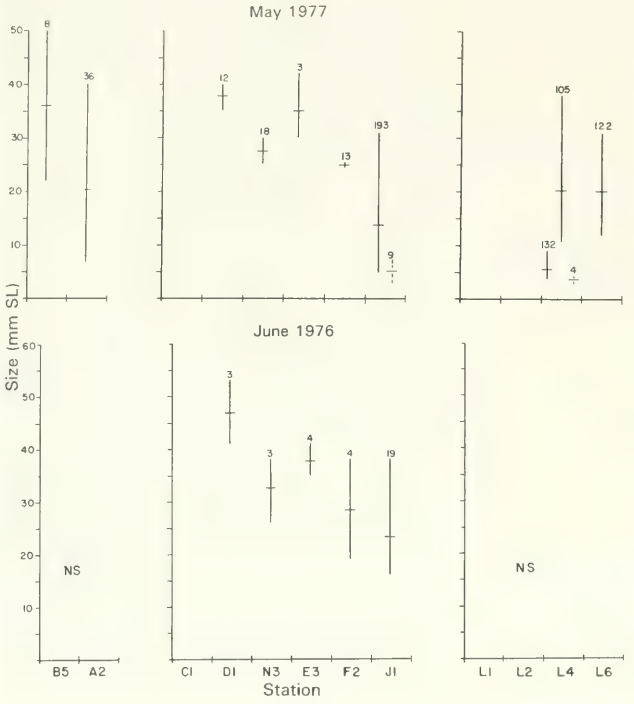

Figure 9

Range and mean size of *Urophycis tenuis* in neuston and bongo collections at stations off Virginia and New Jersey. Solid and dashed lines indicate neuston and bongo collections, respectively. Horizontal bars show mean values. Two neuston ranges are shown if more than one size-class is present. NS = no samples taken; numbers = no. larvae/1000m^3.

pelagic juveniles of southern species into the MAB. Assuming that these individuals are transported northward by the Gulf Stream, it remains to be shown how they leave the influence of this current and move shoreward.

Acknowledgments

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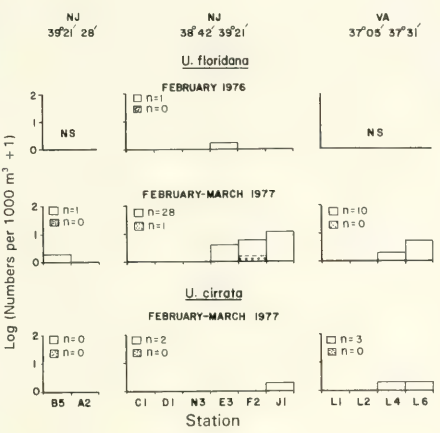

Figure 10

Mean abundance of *Urophycis floridana* and *U. cirrata* in neuston and bongo collections at stations off Virginia and New Jersey, February 1976 and February–March 1977. *n* = actual number of larvae collected. Neuston catches denoted by clear histograms, bongo catches denoted by stippled histograms. NS = no samples taken.

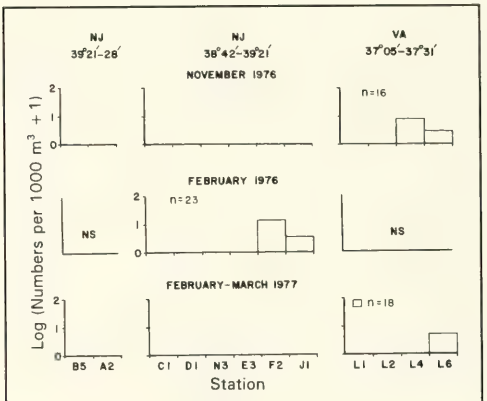

Figure 11

Mean abundance of *Phycis chesteri* in neuston collections at stations off Virginia and New Jersey, during February 1976, November 1976, and February–March 1977. *n* = actual number of larvae collected. Neuston catches denoted by clear histograms, bongo catches denoted by stippled histograms. NS = no samples taken.

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Appendix Table 1

Sources of material, collection data, and lengths of hakes used in radiographic analyses of meristics and pterygiophore interdigitation. Standard acronyms for resource collections follow Leviton et al. (1985).

Species	Collection #	Location	No. specimens	SL(mm)
U. earlli	USNM 025295	N. Carolina	1	124
	USNM 155746	32°34'N,79°05'W	1	55
	USNM 155747	Wilmington, NC	2	50–60
	USNM 226521	32°29'N,79°42'W	3	88–129
	USNM 226522	32°29'N,79°41'W	3	91–122
	USNM 226523	32°29'N,79°41'W	1	113
	USNM 226524	33°14'N,78°24'W	1	130
	USNM 226525	34°14'N,78°24'W	1	82
	USNM 226526	32°28'N,79°42'W	4	91–132
	USNM 226530	32°29'N,79°40'W	4	96–157
	USNM 226531	32°29'N,79°41'W	5	138–166
	USNM 226543	28°48'N,80°38'W	1	74
	VIMS 06557	Gulf of Mexico	1	195
U. floridana	USNM 073010	Key West, FL	1	63
	USNM 116729	Beaufort, NC	16	35–49
	USNM 131586	26°18'N,83°09'W	1	59
	USNM 155738	Texas	1	77
	USNM 155782	Cape Canaveral, FL	1	86
	USNM 155783	St. Augustine, FL	1	67
	USNM 156146	Pelican-Stn. 120–5	1	94
	USNM 214118	Brickhill Creek, GA	5	64–75
	VIMS 03756	Silver Bay	1	165
	VIMS 04142	Brunswick Sound, GA	5	78–113
	VIMS 04152	Silver Bay	4	52–85
	VIMS 04192	Pensacola, FL	2	81–109
	VIMS 04193	Cumberland Id., GA	2	129–184
	VIMS 04194	N.Cumberland R., GA	2	133–157
	VIMS 04195	Santa Rosa Sound, FL	1	66
	VIMS 04196	Oregon S646	1	185
U. cirrata	GCRL 433	29°09'N,88°33'W	1	281
	GCRL 436	29°22'N,87°30'W	1	290
	GCRL 525	29°11'N,88°07'W	3	318–343
	GCRL 2783	Louisiana	4	109–130
	GCRL 17534	28°27'N,90°38'W	1	145
	USNM 115686	22°23'N,91°45'W	1	141
	USNM 116929	Tortugas, FL	1	140
	USNM 155642	29°04'N,88°44'W	1	114
	USNM 218169	29°18'N,88°51'W	1	108
	USNM 218192	28°58'N,84°44'W	1	109
	USNM uncat.	24°32'N,83°36'W	1	197
	USNM uncat.	28°59'N,88°48'W	1	198
	USNM uncat.	28°35'N,91°12'W	2	186–220
P. chesteri	USNM 025903	Newport, RI	17	73–98
	USNM 026081	Martha's Vineyard, MA	5	68–83
	USNM 026097	No data	1	79
	USNM 028732	No data	9	58–76
	USNM 083821	GA, SC	12	54–65
	USNM uncat.	Atlantic Arctus Exped.	6	105–147
	USNM 092695	No data	1	63
	VIMS 05238	36°43'N,74°39'W	4	67–150

Appendix Table 2

A summary of key meristic, morphometric, and pterygiophore interdigitation characters used to separate *Phycis chesteri* and six species of *Urophycis*. Given for each species: length (mm) at which characters are attained (upper), morphometic or meristic value (middle), and explanatory notes (**bold** letters in parentheses). Percentages indicate proportion of a species that possesses a particular character.

	Epibranchial gill rakers	Caudal-fin rays	2nd dorsal-fin rays	1st dorsal-fin rays	Abdominal vertebrae	Anal-fin pterygiophores anterior to first haemal spine	Interdigitation of second dorsal-fin pterygiophore	Body depth at vent as %SL	Height of pelvic-fin base as percent of mandible length	
U. tenuis	11–13 mm 2 (95%) **(A)**	11 mm ≥35 (99%)	14 mm ≥53 (93%)	15 mm ≤12	4 mm ≥15 **(H)**	8–9 mm >6 (2%) <6 (60%)	≥9 (88%) **(L)**	12 mm 19.0–21.1 **(M)**	6–19 mm 24–42 **(N)**	20–34 mm 26–37
U. chuss	11–13 mm 3 (97%)	8–9 mm <35	14 mm ≥53 **(E)**	14 mm ≤12	4 mm ≥15 (87%) **(I)**	8–9 mm >6 (45%) <6 (5%)	12 mm ≥9 (52%)	12 mm 17.6–19.7	6–19 mm 20–39	20–34 mm 15–22
U. regia	11–13 mm 3 (97%)	8–9 mm <35	14 mm ≤52 **(E)**	13 mm <12 **(G)**	4 mm ≤14 **(J)**	8–9 mm >6 (57%) <6 (2%)	12 mm <9	12 mm 18.4–21.7	6–19 mm 19–33	20–34 mm 12–28
U. floridana	2	<35	≥53	13 (33%)	≥15 (98%) **(K)**	>6 (74%) <6 (0%)	>9 (73%)	12 mm 17.7–19.8	15–19 mm 29–36	20–34 mm 23–37
U. earlli	2	<35 **(C)**	>53	<12 **(G)**	≤14 (87%) **(K)**	>6 (85%) <6 (0%)	<9			
U. cirrata	3	<35	>53 **(F)**	≤12	≥15 **(K)**	>6 (0%) <6 (82%)				20–34 mm 31–39
P. chesteri	16–18 mm 4–5 **(B)**	<35 (77%) **(D)**	≥53	≤12	≥15 (88%)	>6 (0%)	>9 (38%)	12 mm 21.0–23.4	6–19 mm 44–74	20–34 mm 46–61 **(O)**

Notes

(A) *U. tenuis* occasionally possessed a third gill raker, but in only one specimen (n=167) were three gill rakers found on both left and right sides.
(B) Three epibranchial gill rakers had developed by 13 mmSL.
(C) *U. earlli* has never been recorded with >31 caudal-fin rays, while all other hake commonly have >31 rays.
(D) Although ranges in *U. tenuis* and *P. chesteri* overlapped, numbers of caudal-fin rays separated over 40% of *P. chesteri* (<34 rays) from more than half of *U. tenuis* (>36 rays).
(E) Numbers of second dorsal-fin pterygiophores separated *U. regia* from *U. chuss* at sizes as small as 6 mmSL. Although not shown here, one specimen of *U. chuss* (n=106) possessed 52 second dorsal-fin rays.
(F) Although ranges overlap, almost 70% of *U. cirrata* had at least 64 second dorsal-fin rays, while *P. chesteri* and other species of *Urophycis* (except *U. earlli*) had <64 rays.
(G) *U. regia* and *U. earlli* have never been found with >10 and 11 first dorsal rays, respectively, while over 80% of *U. floridana* (n=45) possessed >11 rays.
(H) Numbers of abdominal vertebrae helped identify *U. tenuis* larvae <10 mm, the size below which numbers of caudal-fin rays no longer afford confident identifications. See Results.
(I) Numbers of abdominal vertebrae aided in the identification of *U. chuss* in summer collections from the MAB when this was the only species of hake found. See Results.
(J) Only eight specimens of *U. regia* from the Middle Atlantic Bight (n=698) had 15 abdominal vertebrae, and seven of these specimens had an anomalous 15th vertebra.
(K) *U. floridana* and *U. cirrata* commonly possessed 16 or 17 abdominal vertebrae, but *U. earlli* has never been recorded with this many.
(L) Numbers refer to the interneural space into which points the pterygiophore supporting the first ray of the second dorsal fin. The first interneural space was defined as the space anterior to the first haemal spine.
(M) Specimens of all species were cleared and stained.
(N) Size ranges do not define size when character first became useful, but bracket the size-range over which particular morphometric values were found.
(O) At sizes >35 mmSL, *P. chesteri* was similar to *Urophycis* with respect to this character.

Abstract.—The reproductive biology of *Lutjanus vittus*, an important component of the trawl-fishery catch from the North West Shelf of Australia, was determined from random, stratified trawls made every 2 mo during August 1982–October 1983. The smallest mature female was 142 mm FL; half of the females at 154 mm (estimated 1+yr of age) were mature. The major spawning season was from September to April, although some spawning occurred in other months. A semilunar pattern of spawning activity was observed, with peaks in the proportion of spawning females ~3 d after the new moon and 6 d after the full moon. Individuals spawn about 22 times each lunar month. The diel changes in proportion of fish with ripe oocytes and early- and late-stage postovulatory follicles, together with data on maximum oocyte diameter, suggest that most individuals spawn between 11:00 and 15:00 h on peak spawning days. The relationship between batch fecundity (F) and fish fork length (L in mm) was exponential ($F=3.656\times10^{-6}$ $L^{4.093}$) and with fish weight (W, g) was linear ($F=124.2\times W-3081$). Unlike gonad weight, batch fecundity did not decline as the spawning season progressed.

Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia

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Lutjanids are of great importance in fisheries throughout the tropics and subtropics, and *Lutjanus vittus* distributed throughout the Indo-West Pacific is a highly valued component of the multispecies trawl fishery of the North West Shelf of Australia (NW Shelf), comprising ~4% of the total catch of ~165,000 t between 1972 and 1980 (Jernakoff & Sainsbury 1990). Its early life history has been studied in Japan (Mori 1984); its biology, in New Caledonia (Loubens 1980a,b). Information on growth and mortality of this species on the NW Shelf has recently been published (Davis & West 1992). However, there is no published information on the reproductive biology of *L. vittus* that would pertain to the management of this fishery on the NW Shelf.

Some information on the reproductive biology of over 40 species of lutjanids is available (see review by Grimes 1987). Many studies have indicated that lutjanids are multiple spawners, based on the evidence of multimodal size-frequency distributions of oocytes, but techniques such as the hydrated oocyte and postovulatory follicle methods (Hunter & Goldberg 1980, Hunter & Macewicz 1980), for measuring spawning frequency in marine fishes, have not been applied to lutjanids (Everson et al. 1989). In this paper we present data on oocyte development, size-at-maturity of females, and batch fecundity in *L. vittus* from the NW Shelf. We also demonstrate both diel and semilunar spawning periodicity through an analysis of the temporal distribution of hydrated oocytes and early- and late-stage postovulatory follicles, and provide estimates of spawning frequency and annual fecundity.

Materials and methods

Specimens were obtained from the CSIRO North West Shelf program between August 1982 and October 1983 (Young & Sainsbury 1985). Details of the two-monthly random stratified trawl surveys of shelf waters within latitudes 116°E and 119°E are given in Davis & West (1992). A subsample of 20–40 *Lutjanus vittus*, which approximately represented the size-frequency composition of the total catch (Kimura 1977), was selected from each random trawl. Fork length was measured to the nearest 1 mm and total weight to the nearest 1 g. Fish were sexed and up to 200 ovaries per cruise were fixed in 10% formalin in seawater for histological and whole oocyte examination. Additional biological samples were collected from nonrandom trawls to investigate lunar and diel periodicity in spawn-

ing. Samples were also obtained at 4 h intervals during 6–9 October 1988 to further investigate diel periodicity of spawning.

In the laboratory, ovaries were blotted dry and then weighed to the nearest 0.1 g. Whole oocytes were obtained by cutting a complete cross-section 1–2 mm thick from the middle of the ovary, and teasing the oocytes apart with needles. Oocytes were examined in water under a stereomicroscope using transmitted light and brightfield illumination. We measured maximum oocyte diameter (MOD) as the diameter of the largest oocyte (to the nearest 20 μm) in the sample. Because oocytes were basically spherical, the orientation of oocytes with respect to the line of measurement was random.

The size-frequency distribution of oocytes within ovaries at different stages of maturity was determined. Sections 1–2 mm thick were cut from the middle of one ovary, the oocytes teased apart with needles, and further separated by immersion in an ultrasonic bath for ~5 min. Oocytes were pipetted into grooves on a perspex microscope slide and examined on a moving stage attachment on a stereomicroscope at 50×, using transmitted light. Orientation was random. As well as measuring each oocyte, we also noted its appearance so that the stage of development could be assessed.

We used whole-oocyte staging to assess ovarian maturity (Hilge 1977, Forberg 1983, West 1990). Our three-stage scheme (Table 1) differed from Hilge's (1977) in that we distinguished late-migratory nucleus oocytes (Fig. 1b) from yolked oocytes (Fig. 1a) by the presence of some translucence at the periphery of the vitelline area (West 1990). Ovaries with late-migratory nucleus oocytes or hydrated oocytes were considered ripe (Fig. 1c).

The relative gonadal index (RGI) was used to quantify the reproductive cycle (Erickson et al. 1985). This index is independent of body size and is based on the model, $W=\alpha_i S^{\beta_i}$, where W is gonad weight (g), S is ovary-free body weight (kg), and α_i and β_i are parameters estimated for maturity stage i. As β_i did not differ significantly between the three maturity stages (ANCOVA, $F=1.304$, df 2,1046, $p=0.27$), a common β was used.

To study short-term spawning rhythms and to verify whole-oocyte staging, we histologically examined 477 ovaries from one cruise during the height of the spawning season (November–December 1982). Histological sections were 10 μm thick and stained with haematoxylin and eosin. The sequence of oocyte maturation is similar in most teleost species (Wallace & Selman 1981). We used the histological criteria of Yamamoto (1956) for assigning oocytes to developmental stages.

The presence of postovulatory follicles was noted in the histological material. These follicles are readily

Table 1

Whole-oocyte staging scheme in *Lutjanus vittus* based on appearance of the most advanced oocytes (modified from Hilge 1977) and corresponding histological stages (Yamamoto 1956) used to describe ovarian maturity.

Whole-oocyte stage	Histological stage
1 Unyolked	
Transparent with visible nucleus, becoming granular and translucent with increasing size.	**Perinucleolus stage** Cytoplasm purple, outer cell membrane not differentiated at 400×.
Granular, translucent with brownish tinge, becoming darker with increasing size, but not opaque.	**Yolk-vesicle stage** Pale vacuoles (yolk vesicles) and a thin but distinct pink-staining zona radiata both present.
2 Yolked	
Completely opaque except for perivitelline border.	**Yolk-granule stage** Yolk granules appear as pink spheres. Fat vesicles coalesce to form larger vesicles around the central nucleus at the end of this stage.
	Early-migratory nucleus stage Nucleus moves out from center of the cell, being replaced by one or two fat vesicles.
3 Ripe	
Distinguished from Yolked stage when parts of the yolk become translucent.	**Late-migratory nucleus stage** Nucleus moves to the periphery of the cell and some of the yolk granules coalesce.
Oocyte is translucent except for the oil droplet.	**Hydrated-oocyte stage** Yolk granules coalesce to form a uniform pink-staining mass.

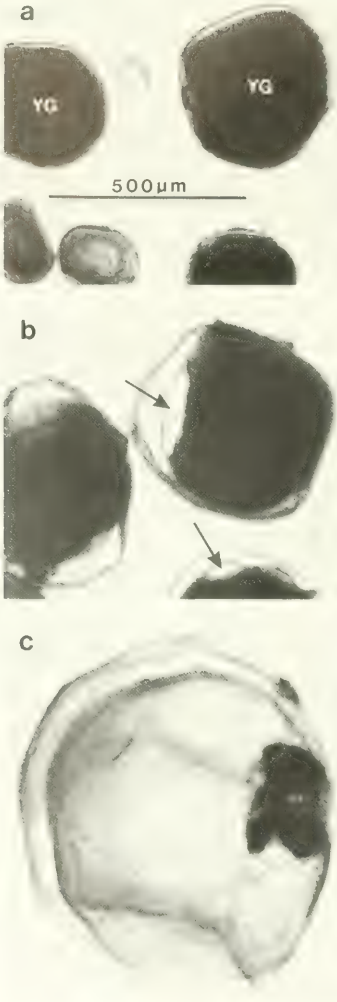

Figure 1
Photomicrographs of whole oocytes of *Lutjanus vittus* representing (a) yolk granule (YG) stage, in which the oocyte is completely opaque except for the translucent perivitelline border; (b) late-migratory nucleus stage, in which parts of the peripheral yolk have coalesced and become translucent (arrowed); and (c) ripe-oocyte stage, in which whole oocyte is translucent, except for the oil droplet. Scale bars 500µm.

identifiable within 12 h after spawning because the folds of the follicle layer are still discrete (Hunter & Goldberg 1980), but they become progressively more compact until they appear as a solid mass of cells. We recorded an early stage where the lumen was open and the wall of the follicle clearly visible (Fig. 2a) and a late stage where the follicle had collapsed and the follicle layer could not be traced around its periphery (Fig. 2b).

Batch fecundity was determined using the gravimetric method (Hunter et al. 1985) to count numbers of hydrated but unovulated oocytes in weighed subsamples of formalin-fixed ovaries. Each subsample consisted of a wedge of tissue extending from the periphery to the lumen of the ovary. In order to estimate the energetic costs of spawning, the dry weight of hydrated oocytes was determined in nine fish. About 100 oocytes were removed from each formalin-fixed ovary. Oocytes

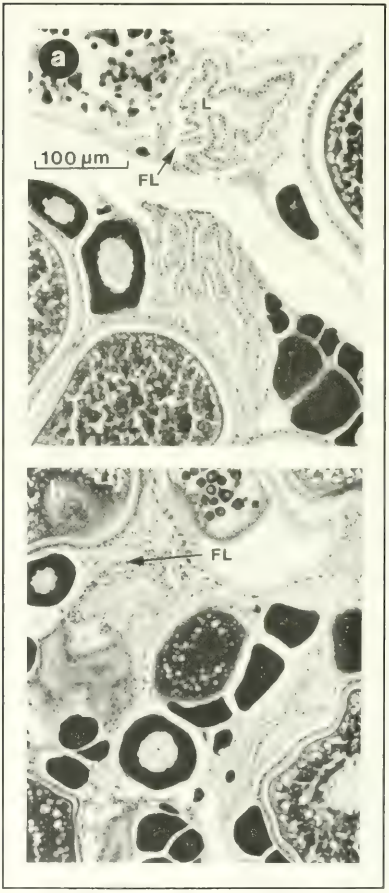

Figure 2
Photomicrographs of transverse section of *Lutjanus vittus* ovary stained with haematoxylin and eosin, showing **(a)** early-stage postovulatory follicles, in which the lumen (L) is open and the folds of the follicle layer (FL) are discrete, and **(b)** late-stage postovulatory follicles, in which the follicle has collapsed and the follicle layer is no longer discrete. FL = follicle layer; L = lumen. Scale bars 100µm.

were washed in freshwater, counted, dried for at least 24 h at 60°C, and weighed to the nearest 0.1 mg.

Size-at-maturity ($L_{0.50}$) was defined as the smallest length at which half of the fish had yolked or ripe-stage ovaries. Weighted least-squares nonlinear regression was used to select the model (Gompertz curve) that best described the relationship between proportion of mature fish and fish length. The simplest model was chosen in which higher parameter models did not significantly improve the fit using the *F*-ratio statistic (Schnute 1981).

RGI's were log-transformed to stabilize variances, and a 2×2 factorial ANOVA was used to test for differences in RGI's between samples collected in August and October and between consecutive years. Differences in RGI over the four periods sampled during the main spawning season (September 1982–April 1983) were tested using ANOVA, and the period effect was partitioned into a linear component and deviations from a linear component to test for trends.

The log-likelihood ratio χ^2 was used to test for independence in contingency-table data (frequency of fish with and without postovulatory follicles by time of day, month, etc.). Cells with expected frequencies <5 were excluded from statistical tests. Repeated-measures ANOVA was used to test for differences in the numbers of eggs/mg tissue taken from the inner and outer walls, and from anterior, middle, and posterior parts of the ovary of five fish. The relationship between log fecundity and log length at different times of the spawning season was examined using ANCOVA.

Results

Maturation of ovaries

Size-frequency and stage of whole oocytes in ovaries representing the developmental sequence of maturation (Fig. 3) indicated that the size of oocytes is correlated with their stage of development but there is considerable overlap between stages. The pattern of oocyte development is asynchronous. Apart from the inference that *L. vittus* is a multiple spawner, the number of spawnings cannot be inferred from modes in the size-frequency distribution (Hunter & Goldberg 1980).

Size-at-maturity

Ovaries were considered mature if their most advanced oocytes were yolked or ripe, as judged by the appearance of the whole oocyte. To avoid including mature fish that had regressed to an unyolked stage towards the end of the spawning season, only data taken between September and February were used. The smallest ripe female observed was 142 mm long (Fig. 4). All fish >220 mm were mature (Fig. 5). The Gompertz curve was fit to the proportion of mature females by 10 mm length groupings:

$$Y(t) = y_\infty e^{-e^{g(t_0 - t)}}, \quad (1)$$

where $Y(t)$ = proportion mature at length t, and y_∞, g, and t_0 are parameters. This provided the best fit with the least number of parameters. The length at which 50% of females were mature ($L_{0.50}$) was calculated to be 154 mm. $L_{0.50}$ is reached at age-1 (Davis & West 1992), and all females at age-3 and older were mature (Fig. 5).

Spawning season

Only data on fish >200 mm were used to describe seasonal changes. The main spawning season appears to be September–April (Fig. 6). The presence of fish with hydrating oocytes throughout the year indicates the spawning season is protracted, although only four fish with hydrated oocytes were collected in June and August 1983. Some mature fish had only unyolked oocytes in their ovaries during April–August (Fig. 6).

The mean relative gonadal index (RGI) peaked in September–October and then declined gradually, reaching its lowest value in June (Fig. 6). There was a marked and significant increase in mean RGI during August–October (2×2 factorial ANOVA, month effect, F=309, df 1,339, p<0.001), with the same increase in both years (interaction effect not significant: F=2.4, p>0.1), and there was a weak but significant difference between years (F=4.3, p<0.05). There were significant differences in RGI between the four periods sampled during the main spawning season, September 1982–April 1983 (ANOVA, F=50.5, df 3,706, p<0.001), predominantly due to a linear component (F=130.1, df 1,706, p<0.001) caused by a decline in RGI over this period (slope –0.236, SE 0.021). On the other hand, there was no significant difference in proportion of ripe fish throughout this period (likelihood ratio x^2 = 6.3, df 3, p=0.10), nor any indication of a decline in the proportion. This suggests that spawning activity remained at about the same level during the main spawning period but that gonads of individual fish were depleted by successive spawnings.

Lunar periodicity in spawning activity

Ovaries of mature fish (n=374) sampled in November–December 1982 were examined histologically for evidence of spawning activity. Data were grouped into 1 d periods according to moon age. Two measures of spawning were used: proportion of fish with postovulatory

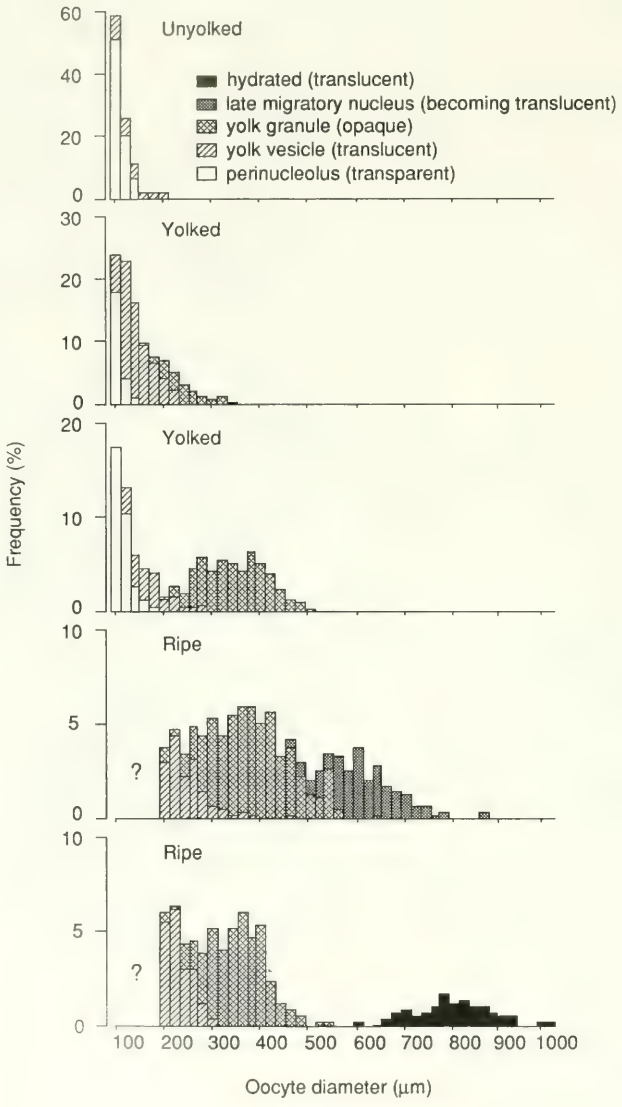

Figure 3

Oocyte size-frequency distribution and oocyte stage, by 20 µm intervals, in *Lutjanus vittus* ovaries representing the developmental sequence of maturation (see Table 1 for details). An ovary classified as Ripe indicates that it contained late-migratory nucleus-stage oocytes or ripe oocytes. Only oocytes >200 µm diameter were measured in Ripe stage-5 ovaries, whereas in other ovaries all oocytes >100 µm were measured.

follicles, and proportion of fish with late-migratory nucleus or hydrated-oocyte stages. The former showed a clear cyclical pattern with two peaks of spawning activity during the month of sampling (Fig. 7). Various sinusoidal curves were fit to the proportion of mature fish with postovulatory follicles sampled each day. The following model, which has a period of 29 d and allows one or two peaks of possibly unequal heights per period, was chosen:

$$y = A+B \sin(x) + C \cos(x) + D \sin(2x) + E \cos(2x), \quad (2)$$

where $t=t/29 \times 2\pi$, and t = moon age (d). A regression weighted by the number (n) in each sample was fit to arcsine (angular) root-transformed data. Proportions of 1 were replaced by $n-1/4$ divided by n. The fitted model accounted for 85.9% of variance in the data. The smaller peak occurred 3 d after the new moon, and the larger peak 6 d after the full moon.

No simple pattern of spawning was apparent from the proportion of fish with late migratory nucleus or hydrated oocyte stages captured each day, presumably because such a pattern was confounded by the effects of time of day (see next section). As postovulatory follicles probably persist for a day, and maybe longer in other species (Hunter & Goldberg 1980, Hunter et al. 1986), their detection does not depend on the time of day of sampling.

Diel periodicity in spawning activity

The November–December 1982 samples were also examined for evidence of diel periodicity in spawning. Only mature fish

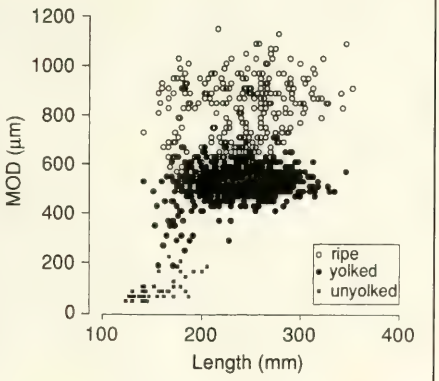

Figure 4

Diameter of the largest oocyte (MOD) of *Lutjanus vittus* by fish length. Ovaries classified as Yolked and Ripe indicate that fish are mature. Data were collected at height of the spawning season (October–February).

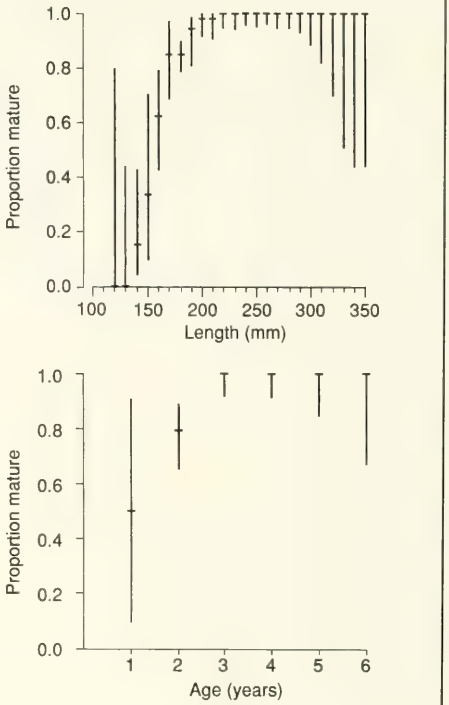

Figure 5

Proportion of total female *Lutjanus vittus* that are mature by 10 mm length-classes and by age-class during the height of the spawning season. Shown are 95% binomial confidence limits. Age data from Davis & West (1992).

caught during days of major spawning activity (lunar days 2–10 and 18–29) were considered. Two measures that proved useful in detecting changes in spawning activity on temporal scales of less than a day were the proportion of mature fish with ripe-stage ovaries based on whole-oocyte staging, and maximum oocyte diameter (MOD).

A clear diel cycle of spawning was evident (Fig. 8). Proportions of ripe-stage fish in samples taken at different times throughout the day were significantly different (likelihood ratio x^2=69, df 7, p<0.001). Proportions of ripe fish were highest between 08:00 and 14:00 h, and no ripe fish were present by 16:00 h. The mixture of ripe and unripe ovaries between 11:00 and 15:00 h could indicate that spawning for that day had already begun and that some of the fish were spent or that only a portion of fish spawned each day. The temporal distribution of MOD showed a similar pattern. Fish about to spawn that day were clearly separable from other fish by MOD at 11:00 h. The MOD's of all but one fish sampled after 15:00 h were the same as nonspawning fish, suggesting that most spawning occurred between 11:00 and 15:00 h on these days, which more or less coincided with rising daytime tides.

Postovulatory follicle data from the same subset of fish also showed a diel pattern (Fig. 9, page 232). The proportion of fish with early- or late-stage postovulatory follicles differed significantly with time of sampling (early-stage likelihood ratio x^2=130, df 7, p<0.001; late-stage likelihood ratio x^2=131, df 7, p<0.001). Fish with early-stage postovulatory follicles were first detected at 12:00 h. By 17:00 h the proportion of fish with early-stage postovulatory follicles had reached its highest level (91%). Thereafter the proportion declined, until by 04:00 h none were present in fish sampled. Late-stage postovulatory follicles followed a similar temporal pattern, with a peak that lagged the early stage by 12–14h. The very few late-stage postovulatory follicles in samples at 17:00 h may have resulted from spawning early that day or late spawn-

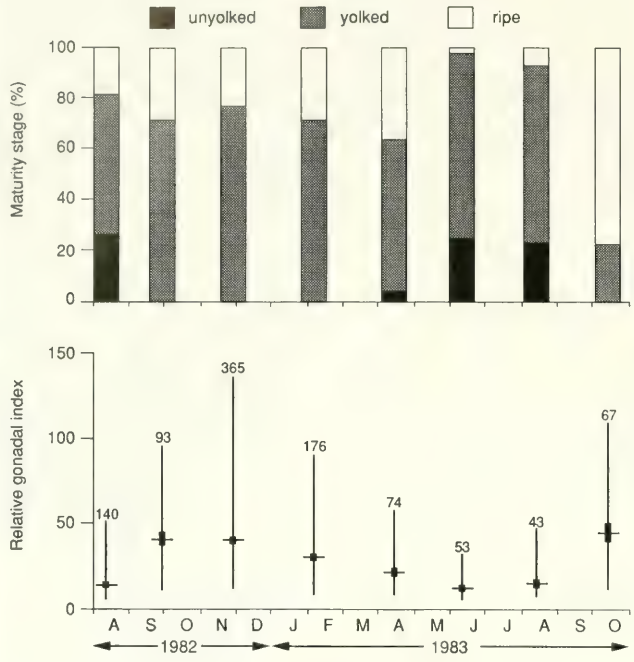

Figure 6

Mean relative gonadal index, 95% confidence limits and range, and proportion of female *Lutjanus vittus* at each maturity stage determined by whole-oocyte staging plotted against the mean date of each sampling period. Number in each sample is shown.

ing on the previous afternoon. In either case, the late stage appears to persist for about 24 h. Only 13% of fish examined from this subset did not have postovulatory follicles, and most of these (74%) were from fish sampled between 09:00 and 15:00 h. This would be consistent with the hypotheses that follicles persist for 24 h or less and that most fish spawn daily during the major periods of spawning activity.

The diel pattern of spawning indicated by data collected in November–December 1982 was supported by further sampling every 4 h over 6–9 October 1988. The proportions of ripe fish in samples taken at different times throughout the day were significantly different (likelihood ratio x^2=110, df 6, p<0.001). Ripe fish were found between 12:00 and 16:00 h (Fig. 10). The temporal distribution of MOD followed the same pattern observed in November–December 1982.

Spawning frequency

As postovulatory follicles in *L. vittus* persist for ~24 h, they provide a good indication of spawning over the previous 24 h and can be used to determine spawning frequency. Parameter A from Eq. 2 provides an estimate of the proportion of females spawning each day averaged over the 29 d lunar cycle. On average, females spawn 21.7 times each lunar cycle (95%CL=19.3–23.9). If we assume that this spawning intensity occurs during October–April, then females spawn at least 150 times each year.

Batch fecundity

In order to determine the most appropriate sites in the ovary from which to take subsamples to determine batch fecundity, the number of eggs/mg tissue was determined for six regions of the ovary of five fish. Wedges of ovary were taken from both inner and outer walls at anterior, middle, and posterior parts of each right-hand ovary. There were no significant differences in numbers of eggs between inside and outside (ANOVA, F=0.016, df 1,4, p=0.91) or anterior, middle, or center (ANOVA, F=1.45, df 2,8, p=0.29) nor any interaction between the effects (ANOVA, F=0.54, df 2,8, p=0.60). A paired t-test indicated that egg counts from a wedge of tissue taken from the middle-outside position did not differ significantly between left and right ovaries (t=−0.008, df 4, p=0.99). Subsequently, batch fecundity was estimated from the mean of three subsamples taken from the anterior, middle, and posterior of either the left or right ovary of 29 fish. The coefficient of variation for estimates from three subsamples was 0.02–0.21, with a mean of 0.11.

The relation between fish length (L, mm) and batch fecundity (F) was best described by the equation

$$F = 3.656 \times 10^{-6} L^{4.093} \quad (F=26.1, \text{ df } 1,27, p<0.001), \qquad \text{(Fig. 11)}$$

and the relation between fish total weight (W, g) and batch fecundity by the equation

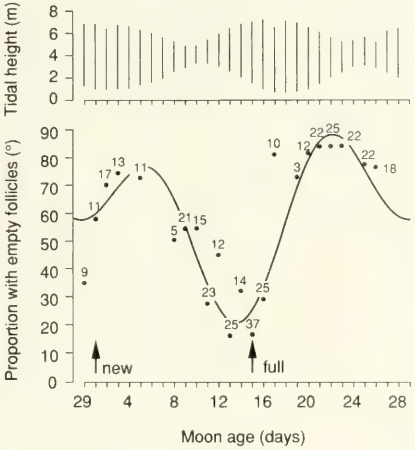

Figure 7

Proportion of mature female *Lutjanus vittus* with early- or late-stage postovulatory follicles plotted against time of sampling (expressed as moon age). A sinusoidal curve with a period of 29 d and two peaks of unequal height were fit to arcsine (angular) root-transformed data. Lunar tide cycle, indicated by maximum and minimum heights of daily tides, has also been plotted, and the number in each sample is shown.

$F = 124.2 \times W - 3081$ (F=17.7, df 1,27, p<0.001).

Batch fecundity varied markedly between fish of the same size. As the data were obtained from four different periods during the spawning season, we tested to see whether the different spawning periods could explain some of the variability in batch fecundity. There is some suggestion that batch fecundity might be higher in November and decline over the spawning season, following the seasonal pattern of RGI (Fig. 11). However, in the regression of log fecundity/log length, the test for homogeneity of slopes between sampling periods was found to be not significant (ANCOVA, F=0.318, df 1,2604, p=0.57), and, assuming a common slope, there was no significant difference in the intercepts for the four periods (ANCOVA, F=1.76, df 1,2605, p=0.19).

Oven-dried weights of hydrated oocytes were determined on 9 fish. Egg weight did not vary with fish length (F=0.28, df 1,8, p=0.61) or with maximum oocyte diameter (F=0.88, df 1,8, p=0.37). The mean dry weight of individual hydrated oocytes was 0.012 mg (SE 0.0005).

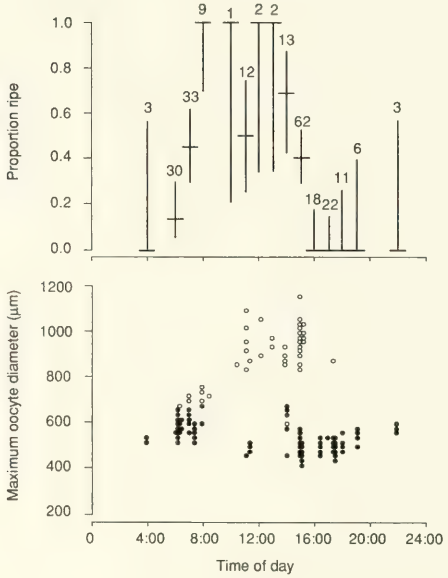

Figure 8

Proportion of mature female *Lutjanus vittus* with ripe-stage ovaries, and maximum oocyte diameter (MOD) in individuals caught at different times of the day. Samples taken during periods of major spawning activity (lunar days 2–10 and 18–29) during November–December 1982. Oocytes have been assigned to ovarian maturity stages: Ripe (○) and Yolked (●). Shown are 95% binomial confidence limits for proportions and number in each sample.

Discussion

The smallest ripe female observed in this study was 142 mm long, which is close to the length-at-first-maturity of female *L. vittus* from New Caledonia (Loubens 1980a). In a review of size-at-first-maturity, Grimes (1987) found consistent differences between insular and continental species of lutjanids and between shallow and deepwater groups in the ratio of length-at-first-maturity to maximum length. Female *L. vittus* clearly fall into the continental shallow group that mature early at ~44% of their maximum length.

The spawning season on the NW Shelf is protracted: While *L. vittus* spawned throughout the year, the major spawning period appeared to be September–April. Loubens (1980a) determined from GSI and visual staging that *L. vittus* spawn during October–February in New Caledonia (Loubens 1980a). *Lutjanus*

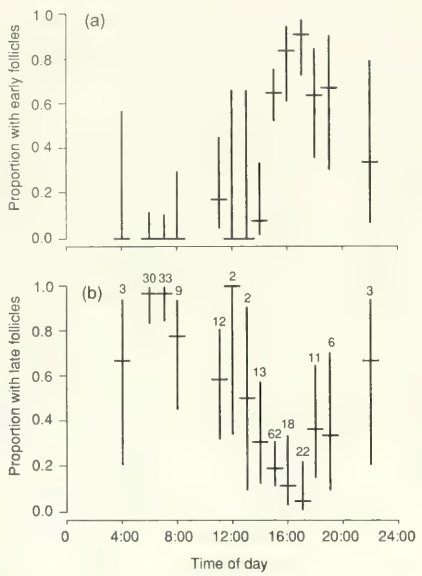

Figure 9

Proportion of mature female *Lutjanus vittus* with **(a)** early and **(b)** late-stage postovulatory follicles plotted against time of sampling. Samples taken during periods of spawning (lunar days 2–10 and 18–29) during November–December 1982. Shown are 95% binomial confidence limits for proportions and number in each sample.

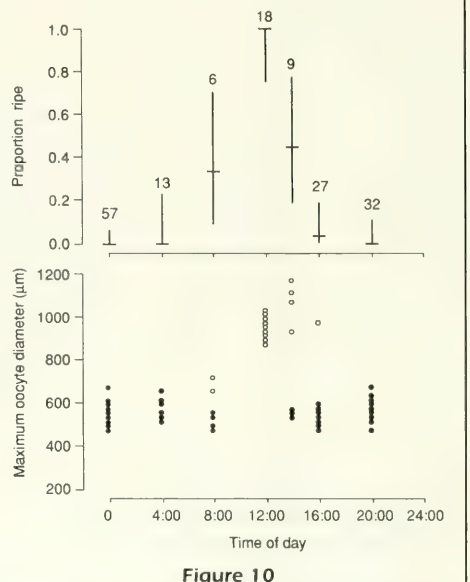

Figure 10

Proportion of mature female *Lutjanus vittus* with ripe ovaries, and maximum oocyte diameter (MOD) of individuals caught at different times of the day. Samples taken during 6–10 October 1988. Oocytes have been assigned to ovarian maturity stages: Ripe (○) and Yolked (●). Shown are 95% binomial confidence limits for proportions and number in each sample.

vittus tends to comply with Grimes' (1987) generalization that continental species, regardless of latitude, have a restricted spawning season.

The pattern of restricted spawning in *L. vittus* may be linked with the production cycle on the NW Shelf, as has been suggested for other continental species of lutjanids (Grimes 1987). The nutrient source is slope-water washing up onto the NW Shelf in summer when the Leeuwin Current is no longer flowing (Holloway et al. 1985, Tranter & Leech 1987). Enrichment is greatest between December and April. In winter the southeast trade winds blow, there is little stratification of the water column, and the plankton are dispersed (Tranter & Leech 1987). These winds abate by late August or early September, enabling the water column to become highly stratified and the plankton more concentrated (Tranter & Leech 1987). This would result in improved feeding conditions for larvae and coincides with the start of major spawning activity.

During the major spawning period, individual *L. vittus* spawn a number of times. Serial spawning has been inferred in a number of lutjanids: *L. purpureus* (De Moraes 1970), *L. kasmira* (Rangarajan 1971), *L. griseus* (Campos & Bashirullah 1975), *L. synagris* (Erhardt 1977), *Pristipomoides multidens* and *P. typus* (Min et al. 1977), *Rhomboplites aurorubens* (Grimes Huntsman 1980), *P. filamentosus* (Ralston 1981), *Etelis carbunculus* (Everson 1984), *E. coruscans* and *Aprion virescens* (Everson et al. 1989). While serial spawning appears to be commonplace in lutjanids, the number of batches of eggs spawned each season has not been determined conclusively for any species (Grimes 1987). Our data suggest that *L. vittus* spawn about 22 times/mo during late November and early December. If this spawning intensity were maintained throughout the whole spawning period (October–April), then most individuals would spawn about 150 times/yr. Even if spawning intensity were half this rate for the remainder of the season, then *L. vittus* would spawn about 90 times/yr.

Greatest spawning activity in *L. vittus* was shortly after the full and new moons. A lunar rhythm in spawn-

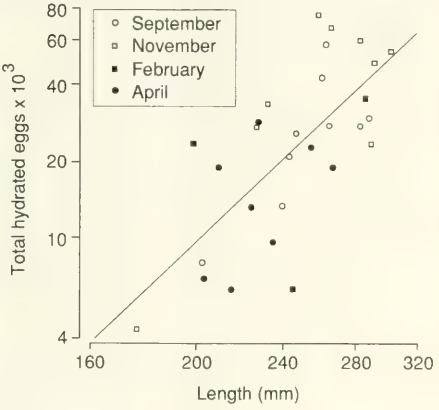

Figure 11
Relation between batch fecundity and fish length of *Lutjanus vittus* at four different spawning periods (scales are logged).

ing has been reported in many teleosts and some lutjanids, with most spawning activity close to the time of the full moon; e.g., *L. vaigiensis* (Randall & Brock 1960), *L. griseus* (Starck 1970), *L. synagris* (Reshetnikov & Claro 1976), *L. kasmira*, *L. rufolineatus*, and *P. multidens* (Mizenko 1984; although aquarium populations of *L. kasmira* spawned at the new and full moon [Suzuki & Hioki 1979]).

Many hypotheses have been proposed to explain why lunar reproductive cycles have developed in fishes (see reviews by Johannes 1978, Thresher 1984, Gladstone & Westoby 1988, Robertson et al. 1990). We cannot adequately explain why *L. vittus* has a well-developed lunar reproductive pattern. Spawning is probably linked to the lunar tidal cycle rather than moonlight per se, as it occurred chiefly after new and full moons and during daylight. The North West Shelf is a region of strong semidiurnal tides which flow predominantly cross-shelf at the shelf break and alongshelf near the coast (Holloway 1983). Spawning during spring tides would therefore disperse the eggs of *L. vittus* alongshelf rather than cross-shelf. There would be a clear advantage for larvae if they were advected to the midshelf or further offshore because these areas have greater productivity (Young et al. 1986). There is, however, no evidence for dispersal offshore; both larvae and adults of *Lutjanus* spp. are primarily found on the inner shelf (Leis 1987).

Frequency of spawning was determined from the proportion of females with postovulatory follicles. Our findings indicate that postovulatory follicles persist for <1 d, whereas studies on other species have found that they persist for <15 h (Takita et al. 1983), <2 d (Hunter & Goldberg 1980, Hunter et al. 1986, Clarke 1987), or slightly longer (Alheit et al. 1984). Our data on postovulatory follicles suggest that females on average spawn about 22 times each lunar month. The proportion of females spawning each day peaks about 3 d after the new moon and 6 d after the full moon.

It seems unusual that *L. vittus* spawns during early afternoon. Thresher (1984) reviewed 22 pelagic egg-producing families, including lutjanids, and found that most spawned around dusk, as did Colin & Clavijo (1988) who examined 26 species associated with coral reefs. Lutjanids produce pelagic eggs (Suzuki & Hioki 1979) and all other reports indicate that they spawn at or after dusk (Wicklund 1969, Starck 1970, Suzuki & Hioki 1979). Possibly spawning is linked to the state of the tide, rather than the time of day per se. In both 1982 and 1988, spawning activity coincided with rising tides; it may have been coincidental that these were during daylight hours.

Batch fecundity increased exponentially with fish length and linearly with fish weight. The variability in batch fecundities did not appear to be due to errors in using the gravimetric method. The mean coefficient of variation of estimates was 0.11, and it never exceeded 0.21. Care was taken to exclude ovaries that had partially spawned (identified by the presence of early-stage postovulatory follicles), and only those ovaries that had a clearly identified mode of partly-hydrated oocytes were used for estimates. Also, batch fecundities did not appear to differ between sampling periods. One might have expected a decline in fecundity as ovary weight declined over the season. Another possible reason for the variability in batch fecundity might have been that samples were taken at different phases of the lunar cycle. However, our data are inadequate to test this hypothesis.

Comparison of the fecundity of *L. vittus* with that of other lutjanids is not particularly useful, due to inconsistencies in methods of estimation and uncertainty as to whether true batch fecundities have been estimated (see review by Grimes 1987). It is, however, useful to consider the energetic costs of spawning by *L. vittus* considering its high annual fecundity. A 300 mm long female *L. vittus* would shed about 7.6 million eggs annually if it spawned 150 times/yr, or 4.5 million eggs if it spawned 90 times/yr. Assuming a calorific content for dried eggs of 25 kJ/g (the mean for a range of gadoids; Hislop & Bell 1987), then the annual energy expended on spawning (not including reproductive behavior) would be ~1300 kJ for 90 spawnings, and 2200 kJ for 150 spawnings. Estimation of reproductive effort or efficiency (egg energy/dietary energy × 100)

requires information on daily ration, which is not available for *L. vittus* and apparently has not been determined for any other lutjanid. *Nemipterous furcosis*, a co-occurring species on the N.W. Shelf, has a daily ration in the wild of 2.3% for 23–29 cm fish (K.J. Sainsbury, CSIRO Div. Fish., pers. commun. 1992). *Epinephalus guttatus* of similar size to *L. vittus* have a daily ration of 4% when fed surplus food once each day in the laboratory (Menzel 1960). Assuming a somewhat generous daily ration of 4% for *L. vittus* and a mean prey energy content of 4.2 kJ /g wet weight (Crisp 1971) would result in an approximate annual reproductive efficiency of 4.8% for 90 spawnings and 8% for 150 spawnings. This is similar to an annual reproductive effort in *Engraulis mordax* of 8–11% (Hunter & Leong 1981), a much smaller, shorter-lived species. The reproductive efficiency of the goby *Pomatoschistus microps* is considered to be among the highest ever calculated (Rogers 1988), although its efficiency was calculated using energy consumed over the 16 wk period of spawning and not the whole year. The reproductive efficiency of *P. microps*, calculated using annual energy intake, would be ~8.7–13.5%. The reproductive efficiency of *L. vittus* is comparatively high considering that this effort is sustained over many years.

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Abstract.—The shape of a size-frequency distribution is the result of age- or size-specific rates of growth and survival, their variability, and seasonal and interannual variation in recruitment. Simulation of size distributions can be used to gain insight into the underlying processes that give rise to observed size structure of organisms in the field, but the utility of this approach depends critically on underlying assumptions. Incorrect judgment of the significance of assumptions can lead to erroneous conclusions concerning the causes of bi- or polymodal distributions.

Using the Brody-Bertalanffy growth model and a constant survival rate, bi- and polymodal distributions can be generated when recruitment is pulsed. Even with as many as 10 recruitment episodes per year, size distributions show several modes. A sampling of the literature indicates that most fish and marine invertebrates have pulsed rather than continuous recruitment; thus, when very little is known about a species, pulsed rather than continuous recruitment would be the better assumption when interpreting the shapes of size distributions.

Our simulations differ from those conducted by Barry & Tegner (1990) who assumed continuous and constant recruitment and focused on changing growth and survival parameters to explain bimodal size structure. These authors also suggested that their analysis was appropriate for interpreting the dynamics of red sea urchins *Strongylocentrotus franciscanus*. We have been documenting settlement of both red and purple (*S. purpuratus*) sea urchins. At La Jolla, California, neither species showed continuous settlement; rather, both species had pulses of settlement in spring 1990 and 1991.

Although age-specific variation in growth or mortality parameters can result in bimodal size distributions, it is more likely that such distributions are caused by seasonal pulses of recruitment.

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Inferring demographic processes from size-frequency distributions: Effect of pulsed recruitment on simple models

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For many organisms, size data are easy to gather and size-frequency distributions are common in the literature. In many cases, they provide the only clues to the underlying dynamics of growth, survival, and recruitment. Thus, it is understandable that an extensive literature exists concerning their analysis. One general research approach has focused on the separation of size distributions into components (e.g., Harding 1949, Cassie 1950, Bhattacharya 1967, Young & Skillman 1975, Macdonald & Pitcher 1979). A second approach has attempted to use size data either to estimate mortality when growth parameters are known (e.g., Beverton & Holt 1956, Smith 1972, Van Sickle 1977ab, Ebert 1981 and 1987, Sainsbury 1982) or to estimate both growth and mortality parameters (e.g., Green 1970, Ebert 1973 and 1987, Saila & Lough 1981, Fournier & Breen 1983, Pauly 1987). A third approach has modeled size distributions to gain insight into the underlying processes that give rise to observed distributions (e.g., Craig & Oertel 1966, DeAngelis & Coutant 1982, Barry & Tegner 1990, Hartnoll & Bryant 1990). Simulations of size distributions are metaphors of the dynamic processes that give rise to actual size distributions. The utility of simulation depends critically on the underlying assumptions. If the significance of any of the assumptions is wrongly judged, one may be led to erroneous conclusions concerning underlying dynamics.

As an approach to explaining bimodal size distributions, Barry & Tegner (1990) presented a deterministic model for the development of size distributions that has seven assumptions: (1) Brody-Bertalanffy growth, (2) constant rate of mortality, (3) constant and continuous recruitment, (4) strict determinism for growth, so $\sigma=0$ for all sizes at an age, (5) strict determinism for survival, so $\sigma=0$ for numbers at an age, (6) population growth rate per individual, r, equal to 0, and (7) a stable size distribution equivalent to a stable age distribution. Bimodal size distributions are not possible with these seven assumptions, yet bimodality is commonly observed. Accordingly, one or more of the assumptions must be violated. Barry & Tegner focused on the assumptions concerning growth and survival and concluded that "...bimodality can develop only from an increase in survivorship with age or an increase in the growth coefficient with age, or both." In particular, they argued that size distributions of red sea urchins *Strongylocentrotus franciscanus* required age- or size-specific changes of the growth-rate constant, K, in the Brody-Bertalanffy equation, the mortality coefficient, Z, in an exponential survival curve, or both.

There are three issues that we would like to explore: (1) Possible causes of bimodal size distributions and, in particular, the consequences of pulsed recruitment, (2) applicability of the Barry & Tegner model to sea urchins in California, and (3) general applicability of the Barry & Tegner model.

Size-distribution simulation

We simulated several size distributions to show how the Barry & Tegner model works. Growth was modeled using the Brody-Bertalanffy equation for individual growth:

$$S_t = S_\infty(1-be^{-Kt}) \quad (1)$$

where S_t= size at time t after birth or settlement
S_∞ = asymptotic size
K = growth rate coefficient

$$b = \frac{S_\infty - S_R}{S_\infty} \quad (2)$$

S_R = size at t=0 when organisms begin to grow according to Eq. 1.

Sometimes Eq. 1 is written

$$S_t = S_\infty(1-e^{-K(t-t_0)}) \quad (3)$$

where t_0 = time at which size would be 0

$$b = e^{Kt_0}. \quad (4)$$

Cohort survival was modeled so that the mortality rate was constant:

$$N_t = N_0e^{-Zt} \quad (5)$$

where N_t = number remaining in a cohort at time t
N_0 = initial number in a cohort
Z = mortality rate coefficient.

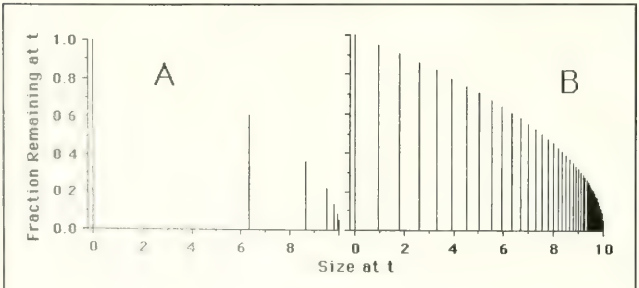

Figure 1
Number (N_t) vs. Size (S_t) where $N_t=N_0e^{Zt}$ and $S_t=S_\infty(1-be^{-Kt})$. **(A)** 1 recruitment event/yr; **(B)** 10 recruitment events/yr.

Equations 1 and 5 were used to generate a number-density distribution that was integrated over segments of arbitrary size to produce a size-frequency distribution. The first step was to calculate sizes at particular ages (Eq. 1) and then to estimate numbers in a cohort that survived to each age (Eq. 5). The number surviving to a specific size was generated using a constant time-interval and Z<K (Fig. 1). The size-intervals shorten because growth follows Eq. 1. For Fig. 1A, the time-interval between recruitment episodes is 1 unit, which, for purposes of this discussion, we call 1yr. Changing the time-interval for reproduction, that is, the number of evenly-spaced reproductive episodes/yr, changes the number and spacing of lines in the graph. In Fig. 1B we used 10 episodes/yr; that is, an interval of 0.1 yr. In our simulation, we assumed that the population was periodically stable and stationary.

Stable and stationary structure for a population with pulsed recruitment means that demographic structure and number of individuals change between recruitment episodes but are the same across episodes. When the same times after recruitment episodes are compared, the age and size structures of the population are the same (stable structure) and the numbers of individuals are the same (stationary structure). The relationship between density and time would be saw-toothed, with an **average** slope of 0, but with increased numbers-at-recruitment and declining numbers up to the point of another recruitment episode. As the number of recruitment events increases, the height of each tooth becomes smaller until it is smooth when recruitment is continuous. The vertical lines in Fig. 1 represent not only the progression of a single cohort through time, but also cohorts that make up the stable and stationary population.

A size-frequency distribution was constituted by summing all lines within an arbitrary interval of 1.0 size units (Fig. 2). With just one reproductive episode/yr (Fig. 2A), size distribution is polymodal. The overall shape of the size distribution, which is formed by drawing an envelope around the distribution, has a negative slope. Over an increasing range of recruitment frequencies, the polymodal nature is preserved, so that with 10 episodes/yr (Fig. 2C) modes still are evident but the overall shape shows a positive slope. When there are 100 episodes/yr, size distribution approaches the continuous form used by Barry & Tegner:

$$NS = \frac{N_0}{KS_\infty}\left(1-\frac{S_t}{S_\infty}\right)^{\left(\frac{Z}{K}-1\right)}. \quad (6)$$

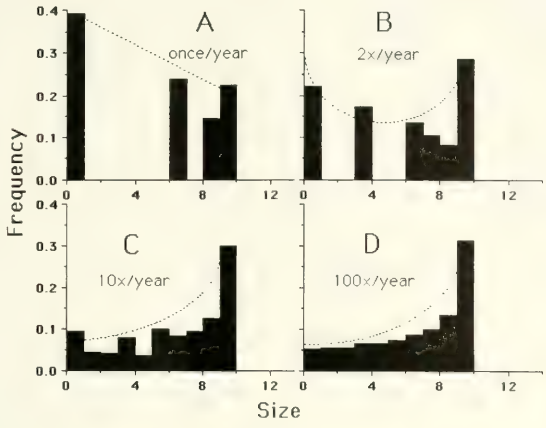

Figure 2

Integration of N_i vs. S_i over intervals of 1.0 size unit. Dotted line emphasizes general shape of the envelope of each distribution. **(A)** 1 recruitment episode/yr; envelope of the distribution has a negative slope. **(B)** 2 recruitment episodes/yr; envelope of the distribution has high points at smallest and largest sizes. **(C)** 10 recruitment episodes/yr; general envelope has a positive slope but has modes at small sizes. **(D)** 100 episodes/yr; envelope has a positive slope.

$$P(x) = \tfrac{1}{2} - r(a_1 t + a_2 t^2 + a_3 t^3) + \epsilon(x) \qquad (7)$$

$$x = \frac{s - \mu}{\sigma} \qquad (8)$$

$$r = \frac{e^{-x^2/2}}{\sqrt{2\pi}} \qquad (9)$$

$$t = \frac{1}{1+Px} \qquad (10)$$

with $a_1 = 0.4361836$, $a_2 = -0.1201676$, $a_3 = 0.9372980$, $p = 0.33267$, and $\epsilon(x) < 10^{-5}$. The area under the normal curve, A, from s to $s+\Delta s$ is

$$A = P(x)_{s+\Delta s} - P(x)_s . \qquad (11)$$

Areas under the normal curve for each cohort were reduced by multiplying each area, A, for a cohort by e^{-Zt} according to Eq. 5. The size-frequency distribution was produced by establishing a 1-unit size-interval and summing parts of all cohorts in each interval.

With one recruitment episode/yr (Fig. 3A), the distribution is polymodal. Because the cluster of individuals that are ≥1 yr is bi-

Simulated size distributions take on an appearance much closer to distributions seen in the field when individual sizes are distributed around mean size-at-age (Fig. 3). A coefficient of variation of 0.1 was used for simulation, so $\sigma = 0.1\mu$. Mean sizes were calculated using Eq. 1, and areas under the normal curve were estimated out to 4σ in units of $\sigma/10$. Areas for each size segment were determined by successive subtraction of terms obtained from a polynomial approximation of the area under the normal curve and based on a program for the normal distribution given by Poole & Borchers (1979), who used an algorithm from Hastings (1955) (Function 26.2.16 in Abramowitz & Stegun 1972). P(x) is the area under the normal curve from the mean, μ, to a size, s, given a standard deviation of σ:

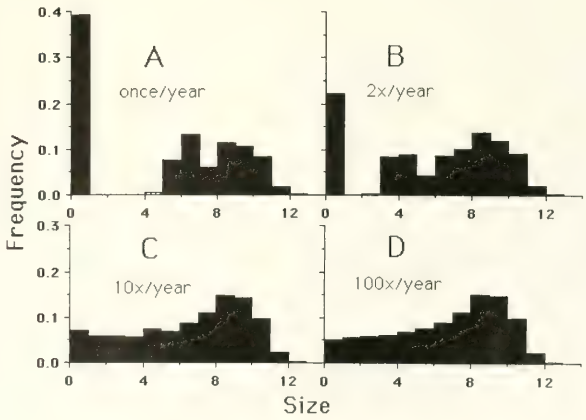

Figure 3

Results of a simulation with Z=0.5, K=1.0, S_∞=10.0, and s=0.1xmean. Simulations differ with respect to number of recruitment episodes/yr (range 1–100/yr). **(A)** polymodal with general envelope with negative slope; **(B)** polymodal with general negative slope; **(C)** polymodality still evident but envelope has a positive slope; **(D)** unimodal with general positive slope.

modal, it is clear that this distribution would always be bi- or polymodal. With two recruitment events/yr (Fig. 3B), the distribution again is polymodal and would always be so. With ten recruitment events/yr (Fig. 3C), the modes begin to disappear but the distribution still is weakly polymodal with modes at 0–1, 4–5, and 8–9 size units. With 100 recruitment events/yr (Fig. 3D), the distribution is unimodal. The general shapes are similar to the distributions in Fig. 2, with slopes that initially are negative (Fig. 3A) switching to positive (Fig. 3C, 3D). A combination of pulsed recruitment, coupled with a decaying exponential growth pattern and low mortality, can lead to size distributions with a wide range of shapes. A panoply of size-distribution shapes can be produced with identical values for Z, K, and S_∞ using different frequencies of recruitment.

Observed settlement of *S. franciscanus* and *S. purpuratus*

Barry & Tegner (1990) used their model specifically to address bimodal size structure in red sea urchins *S. franciscanus*. We disagree with their assumption of continuous recruitment and base this on observed settlement data.

Starting in late February 1990, we deployed settlement collectors at a number of sites along the California coast. Wood-handled scrub brushes (model #0115 National Brush Co., Aurora IL) were used to evaluate temporal and spatial variability in settlement. Brushes were attached as pairs to a line with two pairs per line. The bottom pair of brushes was suspended 1m from the bottom, and the second pair was attached ~20cm farther up the rope. Brushes were tended on a weekly basis at sites within the California Bight and in northern California. One of the sites in southern California was off the end of the pier at Scripps Institution of Oceanography, La Jolla.

Following weekly collection, brushes were placed in a sonic cleaner with seawater for ~3 min to remove animals. Newly-metamorphosed sea urchins have a diameter of ~500 m; thus, following sonication, the water and sediment in the sonicator were strained through 436 m Nitex. Material retained by the screen was then examined using a dissecting microscope, and newly-settled sea urchins were identified and counted.

Settlement at Scripps Pier in San Diego County was confined to a period of about 3 wk starting in late March 1990, and over a longer period in spring 1991 (Fig. 4). Timing of settlement was the same for both *S. purpuratus* and *S. franciscanus*. A few *S. purpuratus* settled in June 1990, but in terms of influencing the structure of a size-frequency distribution, settlement in 1990 can be considered a single event of short duration. Settlement in 1991 began in late February and continued into early June. The important point is that sea urchin settlement at Scripps Pier was seasonal. Settlement at other sites in California, as well as inside and outside kelp beds, all showed seasonal settlement (Ebert et al., in prep.).

Discussion

Bi- or polymodal size distributions and pulsed recruitment are common in the literature. We examined 69 papers that included larval distribution, settlement, or recruitment information for fish, molluscs, annelids, bryozoans, crustaceans, and echinoderms. Out of 216 species, only 8 could be considered to have continuous recruitment, and of these only five spider crab species (Hines 1982) appeared to have constant recruitment; that is, the same number/mo at all seasons. About 98% of the species failed to meet the assumption of constant and continuous recruitment made by Barry & Tegner (1990).

As shown by our simulations, pulsed recruitment produced bimodal distributions that were not transitory in the sense that distributions showed bimodality at all times between recruitment events. However, were a population characterized by pulsed recruitment, sampling could be done in such a manner that the relative magnitude of Z and K could be deduced from a simple

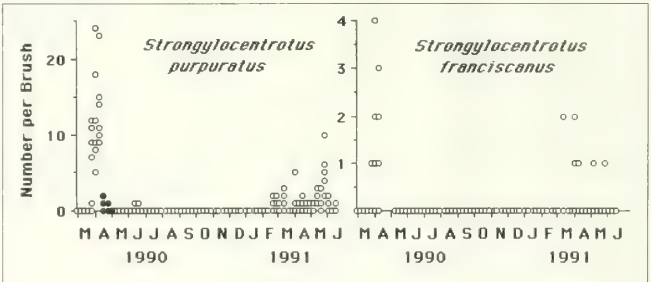

Figure 4

Settlement of purple and red sea urchins, *Strongylocentrotus purpuratus* and *S. franciscanus*, on eight scrub brushes: four suspended 1 m from bottom and four at 1.2 m off bottom at Scripps Pier, Scripps Inst. Oceanogr., La Jolla CA (32°52'N). Solid circles indicate animals not identified to species.

model such as Eq. 6. The changing shapes of the size-frequency distributions for a species with pulsed recruitment could be summed and so be made to approximate the shape that would be obtained with continuous recruitment. To obtain a reasonable approximation, it would be necessary to (1) take many evenly-spaced samples between recruitment events, and (2) weight the samples with the survival rate, e^{-Zt}, from the time of recruitment, t. Weighting could be accomplished if accurate estimates of density were known, which, of course, would be the same as knowing survival. An obvious variant would be the case in which the same area was sampled each time and all individuals were measured. Such a procedure would result in the largest N for the sample immediately following recruitment and the smallest N for the sample just prior to the next recruitment episode. All samples would be pooled before the size-frequency distribution would be constructed.

Approximation of a species with pulsed recruitment to a continuous form could be the same as distributions shown in Figs. 2 and 3. For example, if a species had a single pulse of recruitment and was sampled 10 evenly-spaced times during a year, and each sample was weighted according to the survival rate, then the summed frequency distribution would be C in Figs. 2 and 3. However, if size data were gathered in such a manner that weighting was not automatic, survival rate would have to be obtained by some other technique before size distributions could be summed to approximate continuous recruitment. Techniques for obtaining survival rate, the weighting factor, from size data include those presented by Ebert (1973, 1987), Saila & Lough (1981), Fournier & Breen (1983), and Pauly (1987). It must be noted that analysis of a series of size distributions to obtain the weighting factor would provide information on growth as well as survival, and so there would be scant motivation for constructing a summed distribution.

It is not possible to infer the causes underlying an observed size distribution from a single sample or even from several samples that are widely spaced in time. For example, bimodal size distributions can arise from intra-cohort (e.g., Shelton et al. 1979, Timmons et al. 1980) or inter-cohort (Johnson 1976) competition, and the simple models examined here and in Barry & Tegner (1990) demonstrate that similar size distributions can result from very different mechanisms. In a time-series of size distributions, when the smallest mode shifts through time, the simplest explanation for bimodality is pulsed recruitment (e.g., McPherson 1965, Hickman 1979, Dafni & Tobol 1986/87, Davoult et al. 1990). If sampling is adequate and the smallest mode of a bimodal distribution does not shift during the year (e.g., Gladfelter 1978), the most probable explanation is continuous recruitment coupled with high mortality rates for the smallest animals and improved survival with increased size, which is a case that fits the explanation for bimodality provided by Barry & Tegner (1990). When size distributions are bi- or polymodal and are presented without a time-series (e.g., Tegner & Dayton 1981, Stein & Pearcy 1982, Wilson 1983), reasonable hypotheses can be formulated, but testing requires additional data.

There are numerous examples of pulsed recruitment for sea urchins in California. Size-frequency distributions gathered for purple sea urchins at Papalote Bay, Baja California, Mexico (31°42') (Pearse et al. 1970) may indicate multiple settlement events each year during 1962–69 because samples from January, April, and June–November all had a mode <1.0 cm (Pearse et al. 1970, Ebert 1983). However, if growth was very slow at Papalote Bay, as also indicated by the size-frequency distributions, a single settlement episode would explain the data because individuals with a mode at 0.5 cm were observed only in summer and fall samples.

Published size data for sea urchins at Whites Point (33°43'N) and Point Vicente (33°44'N) during 1966 and 1967 (Pearse et al. 1970) show recruitment pulses for both species of *Strongylocentrotus* and for *Lytechinus*. Recruitment was better in 1966 than in 1967, and small individuals were collected in September 1966 as well as in July and August 1967. Recruitment was not continuous at either Whites Point or at Point Vicente.

Finally, our results showing pulsed settlement for red and purple sea urchins corroborate the observation of a single spike of settlement at Naples Reef (34°25'N) off Santa Barbara in May 1986 (Rowley 1989) and the report by Harrold et al. (1991) of two recruitment events during a year in central California. The pulsed nature of recruitment means that analysis of size-frequency distributions of *Strongylocentrotus* spp. should not be based on a model that explicitly requires continuous and constant recruitment (Eq. 6).

We have demonstrated that by using fixed growth and survival parameters, it is possible to generate a wealth of size-distribution shapes merely by changing the number of recruitment episodes/yr. We have intentionally focused on this aspect of size-distribution shape because we believe that it forms the stumbling block to the application of the Barry & Tegner model. In effect, their model does not provide a convenient way of gaining insight into demographics because, in order to use it to divine the relative magnitude of parameters, it would be necessary to demonstrate the pattern of recruitment for the population being studied. Since the preponderance of field evidence indicates that recruitment generally is pulsed, one cannot "...draw inferences concerning the demographic dynamics of a population...simply by observing the shape of its size-

frequency distribution" (Barry & Tegner 1990). Furthermore, classifying populations as "growth dominated" or "mortality dominated," as these authors have done, introduces terms that obscure rather than illuminate the analysis of size distributions, much in the manner of r- and K-selection comparisons.

Size data should be part of every demographic study because they contain a record of the recent past history of a population. Such data ultimately can be used to estimate parameters, such as Z in Eq. 5, that frequently are difficult to obtain, or to test assumptions concerning annual variability in recruitment or mortality. There currently is no substitute for population studies that include not only size data but also independent estimates of growth and, where possible, survivorship.

Acknowledgments

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Abstract.—Patterns in oocyte development, batch fecundity, and spawning frequency were assessed for black drum *Pogonias cromis* from Louisiana. We identified histological oocyte stages present throughout a protracted breeding season in 1986–87. We observed vitellogenesis beginning in November, and first postovulatory follicles were detected in February. Atresia of yolked oocytes was complete in May. We detected recruitment of vitellogenic eggs after the onset of spawning, suggesting indeterminant total fecundity. Mean batch fecundity for a 6.1 kg female (mean size sampled with hydrated oocytes) was calculated to be 1.6 million hydrated oocytes. A field estimate of spawning frequency was 0.311, indicating that a female spawns on average once every 3 d during the breeding season. Sex ratios were skewed with respect to sampling gear during the breeding season, suggesting segregation of actively-spawning fish on the spawning grounds.

Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana

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The black drum *Pogonias cromis* ranges from Argentina to the Bay of Fundy (Sutter et al. 1986) and is the largest sciaenid, up to 66 kg (Hildebrand & Schroeder 1928). A maximum age of 43 yr was recorded for black drum in the northern Gulf of Mexico (Beckman et al. 1990). Fishing pressure on black drum was historically very low, but has increased with commercial landings in the Gulf of Mexico rising from 1.9 million kg in 1982 to 4.8 million kg in 1987 (NMFS Natl. Fish. Stat. Office, New Orleans LA 70130).

Many temperate fishes are serial spawners with variable production of clutch sizes (Hunter & Goldberg 1980, DeMartini & Fountain 1981, Conover 1985). In particular, large long-lived species may exhibit high variability in reproductive output (Ware 1982). An important management objective with long-lived species is to identify changes in population egg production associated with the harvest loss of older age-classes. For black drum, the potential for exploitation of older age-classes is increased with development of the commercial fishery (NMFS 1986).

Despite the commercial value of black drum, relatively little is known of many life-history aspects of this species (Sutter et al. 1986). In the northern Gulf of Mexico, the spawning season has been reported from late-fall to spring, based upon egg and larval distributions (Jannke 1971, Holt et al. 1985, Ditty 1986) and occurrence of gravid females (Cody et al. 1985). Peters & McMichael (1990) reported peak spawning in March from Tampa Bay, Florida, based on distribution of larvae and juveniles. Murphy & Taylor (1989) computed size-at-maturation to be 590 mm and 650 mmFL for males and females, respectively, although there have been accounts of small females (<350 mmFL) with developing ovaries (Simmons & Breuer 1962, Pearson 1929). Spawning locations have been reported to occur within estuarine bays and in open coastal waters (Pearson 1929, Simmons & Breuer 1962, Jannke 1971, Peters & McMichael 1990). There has been only one estimate of fecundity determined from a single female (Pearson 1929), and no previous estimate of spawning frequency has been made from the adult stock.

Our objective is to provide baseline reproductive information from 1986–87 to be used in assessing popula-

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tion changes and potential egg production to maintain future fishing harvests. We characterize ovarian development, seasonal spawning duration, and frequency as determined by ovarian histology and batch fecundity in Louisiana coastal waters.

Materials and methods

We sampled black drum monthly from commercial landings during March, June, July, October, November, and December 1986 and July 1987 to obtain reproductive information. We increased sampling effort during the period of reported peak seasonal reproductive activity and sampled 25 commercial landings during February, March, April, May, and June 1987. We also sampled recreational hook-and-line landings during March and July 1986 and April 1987. Landings sampled from inshore waters (bays and sounds) were primarily taken by gillnet, haul-seine, and hook-and-line. Landings sampled from offshore waters were taken by trawl and purse-seine.

In order to contrast size-at-maturity with other studies, we made gross visual classifications of gonads during sampling. Macroscopic characteristics for classifying gonads as mature correspond to Bagenal (1968) and Nielson & Johnson (1983). Female characteristics included the presence of eggs visible to the naked eye and light-yellow to reddish appearance from increased vascularization of the ovary. Characteristics for mature males included white appearance and relative enlargement of testes within the body cavity. Measurements included fork length (FL), sex, gutted (viscera removed) body weight (BW), and gonad weight (GW; wet weight blotted dry to nearest 0.1 g). We documented reproductive development by expressing gonad weight as a function of body size using the gonosomatic index (GSI) (Htun-Han 1978, Nielson & Johnson 1983).

We held gonads in ice up to 24 h after sampling and then fixed gonads in 10% formalin. One tissue sample was randomly selected from the preserved ovary and placed in an OmniSette tissue cassette. For histological observation, tissue samples were dehydrated, embedded in paraffin, sectioned, stained with Gill's hematoxylin, and counter-stained with eosin*. We classified oocytes from the prepared histology slides following Wallace & Selman (1981), DeVlaming (1983), and Selman & Wallace (1986). These stages include primary growth (PG), cortical alveoli (CA), vitellogenesis (V), and hydration (H).

To determine relative frequency of oocyte stages, we located a random starting point on a histological section and counted and staged all identifiable oocytes within a field before moving to a new microscope field using manual stage drive. Field movement was inward along the ovigerous lamellae, from the outer tunica albuginea toward the center of the ovary, with realignment along a vertical axis. To be counted, >50% of an oocyte must have been within a field of view. We counted and staged a minimum of 200 oocytes from each female and expressed tallies of the four oocyte stages as a percentage of the total count (Htun-Han 1978, Holdway & Beamish 1985). The Bioquant IV image analysis system software, IBM PC, and Houston Instrument digitizing pad (Hipad model DT-11) were used in conjunction with an Olympus microscope (with video attachment) to facilitate counts and measurements.

In addition to relative frequency of developmental stages, we classified each histological section for the presence of postovulatory follicles (POF) and atretic oocytes to aid in determination of spawning frequency. Our atresia classification was modified from that for northern anchovy (Hunter & Macewicz 1985). If no atresia of yolked oocytes was observed, we denoted the ovary as atretic state 0. Tissue sections exhibiting yolked oocytes undergoing atresia at <50%, >50%, and 100% were classed as atretic states 1, 2, and 3, respectively.

To estimate oocyte development rate, we related our histological observations of actively-spawning black drum to published accounts of spawning time of black drum (Mok & Gilmore 1983, Holt et al. 1985) and rates of hydration and postovulatory follicle degeneration in sciaenids (DeMartini & Fountain 1981, Brown-Peterson et al. 1988). With this time-calibrated histological information, we estimated the hours from spawning for females displaying yolk coalescence, hydration, postovulatory follicles, and atresia, and classified day-0, day-1, and nonspawning females. Our estimate of seasonal spawning frequency was determined by taking the average of the fractions of day-0 and day-1 spawning females relative to total females observed histologically with vitellogenic oocytes. Batch fecundity, the number of hydrated oocytes which comprise the leading "batch" of eggs immediately prior to spawning, was determined from formalin-fixed tissue samples taken from each visibly-hydrated ovary. We took replicate ovarian tissue samples (1–2 g) from anterior, mid-, and posterior regions of left and right lobes. In order to obtain 100–300 hydrated oocytes, tissue subsamples of 90–100 mg (weighed to the nearest 0.05 mg) were placed on a slide, glycerin added, and hydrated oocytes counted (Hunter et al. 1985). After observation of histological sections, any ovaries

* Preparation of histological slides, including washing, embedding, sectioning and staining, were completed by the Louisiana State University School for Veterinary Medicine, Department of Pathology.

with postovulatory follicles, indicating onset of spawning and possible shedding of eggs, were eliminated from further analysis of fecundity. To determine the precision of batch fecundity methodology (Hunter et al. 1985), we compared oocyte counts per unit weight within ovaries using a two-way analysis-of-variance model, SAS GLM procedure (SAS 1985).

Results

Sampling, sex ratio, and maturity

We recorded information on length, sex, and gear for 236 male, 108 female, and 36 immature black drum. In addition, we collected capture data, ovarian samples, and measurements, including somatic and gonad weights used for GSI analysis, from 198 males and 296 females. Ovarian histology sections were made from 234 mature females randomly sampled through June 1987, and were used to determine relative frequencies of oocyte stages (Fig. 1). Of these females, 25 were visibly hydrated, possessed no postovulatory follicles, and were used to estimate batch fecundity. Our sample mean length was 761 mmFL, with adults measuring 650–900 mmFL comprising 89% of individuals used in the study.

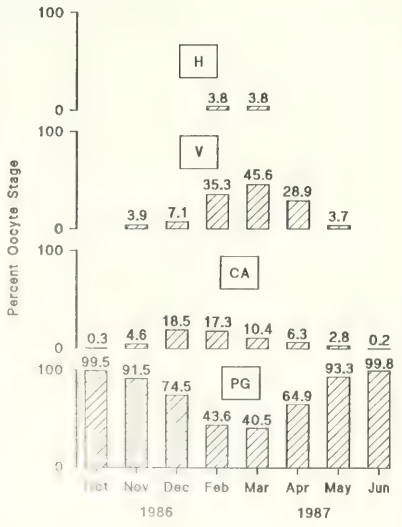

Figure 1

Percent oocyte stage by month for 1986–87 based on point counts of ~200 oocytes/female black drum *Pogonias cromis*. Stages include primary growth **(PG)**, cortical alveolar **(CA)**, vitellogenic **(V)**, and hydrated **(H)**. Number of females examined = 22 Oct, 23 Nov, 23 Dec, 69 Feb, 32 Mar, 24 Apr, 22 May, 19 June.

We found apparent differences in sex ratios from inshore landings (gillnet and haul-seine) and landings from an offshore trawl fishery during the reproductive season (Table 1). Trawl catches were dominated by males, while gillnet and haul-seine samples were dominated by females (Table 1). For months just before and after the reproductive season (October, June, July), females also dominated gillnet and haul-seine landings, but ratios were less divergent. The trawl fishery was not active at these times, but samples of offshore fish were taken from a purse-seine landing (June 1986) and numbers of females and males were nearly equal (0.92:1.0). We applied a χ^2 contingency analysis to test sex ratios by gear type. The χ^2 statistic was significant during the reproductive season (December–May), leading to rejection of the null hypothesis that gear type and sex ratio are independent (Table 1). We assumed that gears were not selective for sex but reflected actual sex ratios in the localities fished. Therefore, the skewed sex ratio suggests a segregation of sexes during the reproductive period. Female: male ratios were more divergent for commercial gears during the months of November–May than October, June, and July (Table 1).

Males and females were first mature at 600–640 mmFL as defined by the size at which individuals exhibit developing and mature gonads from gross visual inspection (Nielsen & Johnson 1983). All black drum >640 mm were mature. All fish <590 mm were immature, but sample size during spawning season was small (n=18 females and 11 males at 460–590 mm).

Table 1

Chi-square contingency analysis of black drum *Pogonias cromis* sex ratios for commercial gears represented by a minimum of 20 individuals.

Gear	Observed			Female:Male ratio
	Male	Female	Total	
Nov, Dec, Feb, Mar, Apr, May (χ^2=79.5, df 2, p<0.001)				
Gillnet	42	105	147	1:0.4
Haul-seine	39	65	104	1:0.6
Trawl	267	126	393	0.47:1
Total	348	296	644	
Oct, June, July (χ^2 =1.18, df 2, 0.9<p<0.5)				
Gillnet	27	42	69	1:0.64
Haul-seine	27	31	58	1:0.87
Purse-seine	13	12	25	0.92:1
Total	67	85	152	

Seasonal oocyte development

Ovaries were characterized by dominance of a single population of primary growth (PG) oocytes year-round, with subsequent appearance of more advanced vitellogenic oocytes during the reproductive season. Cortical alveolar (CA)-stage oocytes, signaling onset of development, were first observed in October 1986 (Fig. 1). By November, CA and vitellogenic (V) stages were common among females and comprised 4.6 and 3.9%, respectively, of the ova counted. We noted increasing proportions of CA and V oocytes relative to counts of PG oocytes by December (Fig. 1). Cortical alveolar-stage oocytes peaked during December, and vitellogenic oocytes lagged in time, exhibiting a peak in March (Fig. 1).

We noted evidence for onset of spawning in 2 females displaying yolk coalescence of vitellogenic oocytes during November 1986. We found conclusive evidence of active spawning on 16 February 1987, when we detected hydrated oocytes (H) and postovulatory follicles (POF). No fish were caught during January 1987 due to bad weather, and there was no evidence of active spawning (i.e., atresia or postovulatory follicles) from samples examined from November, December, or early February (n=61 females). Based on the number of females containing hydrated eggs, spawning peaked in February and March (Fig. 1). Although hydrated oocytes were not detected in April (Fig. 1), presence of postovulatory follicles indicated some spawning was still occurring (Table 2). Coalescence of vitellogenic oocytes, preceding hydration and ovulation, was detected in one female sampled 12 May 1987 (Table 2).

We observed a low proportion of atretic yolked oocytes among females during the development phase prior to onset of spawning. These were similar in appearance to atretic oocytes classified by Hunter & Macewicz (1985) as alpha-stage atresia. A low incidence of atretic yolked oocytes is considered normal during ovarian development in teleosts (DeVlaming 1983). However, we noted an increase in the presence of atretic material as the reproductive season progressed. By 24 April, 13 out of 16 sampled females were classified as atretic state 1, with atretic oocytes <50% of yolked oocytes present. We noted incidence of atretic oocytes >50% of the total yolked oocytes from individuals sampled 12 May 1987, probably signaling a decline in spawning (atretic state 2). By this date, all yolked oocytes were undergoing atresia in 12 out of 22 females examined histologically, and all 22 females exhibited some atretic yolked oocytes. By 12 June, atresia of yolked oocytes was complete for all females examined (n=19), and only gonadotropin-independent PG oocytes remained (atretic state 3).

Table 2

Number of female black drum *Pogonias cromis* in reproductive condition based on histological staging for determination of spawning frequency. Day-0 designated females were actively spawning or close to onset of spawning. Day-1 designated females have been sampled at least 6 h after spawning (see Fig. 3).

Date	Day-0 spawning females	Day-1 spawning females	Total mature females*
11/11/86	2		23
12/16/86	5		23
02/03/87	9		15
02/16/87	19		22
02/20/87	18	5	20
02/24/87			2
02/27/87	6	6	12
03/06/87		4	4
03/23/87	13	12	16
03/27/87	4	10	10
04/06/87		1	8
04/24/87	3	2	16
05/12/87	1		22
Total	80	40	193
Proportion of total	0.415	0.207	
Average proportion of total	0.311		

*Total observed histologically with vitellogenic oocytes

The gonosomatic index (GSI), which is gonad weight expressed as a fraction of body weight, is a common measure of gonad development used to document seasonal changes (Nielson & Johnson 1983). We observed a marked peak in GSI for both males and females in March (Fig. 2). Females exhibited the most dramatic change in gonad weight as the season progressed, with mean gonad weight increasing to >8% of eviscerated body weight. Both sexes followed a similar pattern with respect to time of onset, peak, and decline of GSI (Fig. 2). The gonosomatic index corresponded well with histological observations (Figs. 1, 2). Females exhibited an increase in GSI above "resting" levels in November, when CA and V oocytes were present. Monthly peaks in GSI during February and March resulted from the presence of hydrated oocytes and an increase in the proportion of vitellogenic eggs. Increased atresia of yolked oocytes observed histologically in April and May, associated with decreased spawning, produced a decrease in GSI (Fig. 2). In June, when all yolked oocytes were atretic, female GSI had dropped to 0.87,

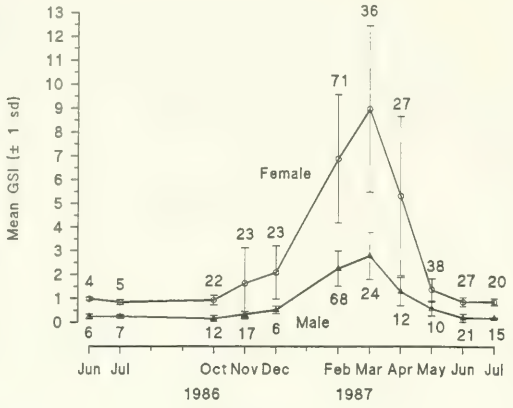

Figure 2

Mean value for gonosomatic index (GSI) for adult black drum *Pogonias cromis* (±1 SD). Sample sizes are indicated by numbers on graph.

and female GSI reached the observed minimum value of 0.84 by July (Fig. 2).

Spawning frequency

In order to estimate proximity to time of spawning and designate females as day-0 and day-1 spawners for spawning frequency calculation (Table 2), we constructed a time-scale of coalescence-stage oocytes, hydrated oocytes, and postovulatory follicles based on literature reports and our observations (Fig. 3). From previous work on related sciaenids, it is known that lipid coalescence, germinal vesicle migration, and yolk coalescence occur beginning in morning samples with hydration becoming evident as the day progresses (DeMartini & Fountain 1981, Fitzhugh et al. 1988, Brown-Peterson et al. 1988). Although exact capture times for some black drum were not known, females exhibiting germinal vesicle migration and yolk coalescence were commonly taken in haul-seine and gillnet sets which were typically landed during morning hours.

A follicle, comprised of an inner layer of epithelial granulosa cells and an outer layer of thecal cells, surrounds each hydrated oocyte. Following ovulation, POFs were present as the evacuated follicle remaining in the ovary. Recent POFs were denoted by linear arrangement of the granulosa cell layer and apical location of very prominent nuclei. These cellular arrangements imparted the appearance of a well-defined lumen and convoluted shape to the POF and were observed from ovaries sampled between 2400 and 0300 h from preliminary samples taken by hook-and-line in March 1986. We concluded that spawning occurred earlier that same night, and used these March 1986 samples as an example of recent POFs. Three females sampled from trawl landings in 1987 with recent POFs also had fully-hydrated eggs in the lumen of their ovaries, indicating active spawning and coinciding with reports of onset of spawning after dusk (Mok & Gilmore 1983, Holt et al. 1985). From interviews of commercial fishermen, capture of black drum in trawls often occurred after dusk and throughout the night, with fish being placed into ice as they were captured. We routinely sampled black drum the morning following their capture, and therefore it is likely that the recent POFs we observed are from fish captured up to 8 h after spawning (Fig. 3).

Over the 1986–87 spawning season, we sampled limited numbers of females bearing POFs (50 females taken from 8 different samples) indicating that duration of POFs may be brief. Hydration-stage oocytes, occurring together with visibly-degenerated POFs, were evident in only 19 females. Additionally, only 1 female contained recent POFs as well as degenerating POFs. Older degenerating POFs were similar in appearance to 24 h-old follicles illustrated in Hunter et al. (1986) from skipjack tuna *Katsuwonus pelamis* spawning at 23–24°C. Therefore, POF duration may be limited to 24–48 h following ovulation (Fig. 3).

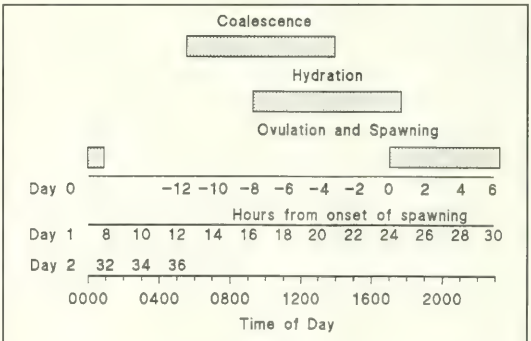

Figure 3

Generalized time-scale of final oocyte maturation and spawning of black drum *Pogonias cromis*, determined from observations and literature reports (see text).

We estimated spawning frequency by examining ovarian tissues of 193 mature females (vitellogenic oocytes present) sampled over the spawning season. We define spawning season as the period during which spawning condition was histologically evident, from first evidence of coalescence of vitellogenic oocytes on 11 November 1986, until atresia of vitellogenic oocytes was occurring in all females encountered on 12 May 1987 (Table 2). The numbers of day-0 and day-1 spawning females was 80 and 40 (frequencies = 0.415 and 0.207) for this period, respectively. This resulted in an overall seasonal frequency of 0.311, or each female spawning on average once every 3 d (Table 2). From November 1986 through May 1987, 50 of 193 females (26%) contained POFs. This method of estimating spawning frequency would correspond to a spawning frequency of once every 4 d, or a total of 46 times, during the spawning season.

Batch fecundity

We determined batch fecundity for 25 visibly-hydrated females which possessed no recent POF in histological sections that would indicate egg shedding. The range in batch fecundity was 7.4×10^5 hydrated oocytes for a 4.3 kg female, to 3.8×10^6 hydrated oocytes for a 4.8 kg female, indicating wide variation in fecundity based on body size (Fig. 4). The number of hydrated oocytes/g of ovary weight ranged from 1046 to 4902. Based on eviscerated body weight, the number of eggs/g ranged from 131 to 793. The mean value for batch fecundity was 1.6×10^6 for a mean eviscerated weight of 6.1 kg.

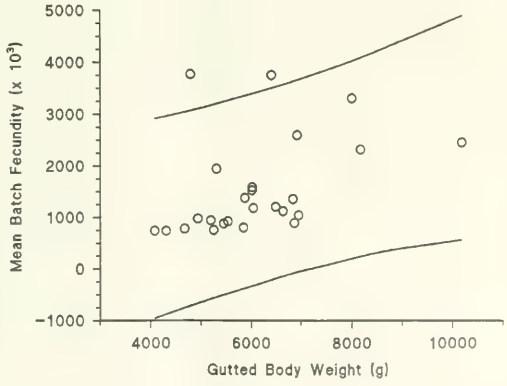

Figure 4

Batch fecundity and eviscerated body weight with 95% confidence interval for hydrated female black drum *Pogonias cromis*, sampled in February and March 1987.

Location of tissue samples

Black drum possess relatively large gonads for teleosts, and we sampled ovaries weighing 0.4–1.6 kg laden with hydrated oocytes. No significant differences were detected between positions within a lobe or between right and left ovarian lobes for number of hydrated oocytes/g of ovarian tissue (Table 3). However, counts of hydrated oocytes/g were lower for the anterior position ($\bar{x}$ 1780) than for either mid- or posterior ovarian regions ($\bar{x}$ 2013 and 1928, respectively) (Table 3).

Discussion

We noted differences in sex ratios between samples collected by various fishing gears during the period of reproductive development and spawning, November–May. Landings by offshore trawlers (where spawning females were found in February and March) were clearly dominated by males. Females dominated in inshore samples from all gears (primarily gillnet and haul-seine landings), but this female dominance was not as prevalent outside the breeding season during October, June, and July. These divergent ratios suggest sexes are spatially segregated for periods during the reproductive season. This difference in sex ratios has been noted in other fisheries where a higher proportion of males attend those females in active spawning condition on the spawning grounds (DeMartini & Fountain 1981, Hunter & Goldberg 1980).

In a synthesis of previous studies, Simmons & Breuer (1962) reported age-at-maturity for black drum to be 2 yr at 320 mm based on scale increments, length frequencies, and gross assessment of ripe females (granular roe observed) in Texas waters. Pearson (1929) found drum as small as 270 mm with developing ovaries. Murphy & Taylor (1989) provide evidence for larger sizes-at-maturity, with males maturing at 590 mm (4–5 yr old) and females maturing at 650 mm (5–6 yr old). Our findings of age-at-maturity agree with Murphy & Taylor's (1989) estimates. Mature females and males occurred at a size-range of 600–640 mmFL, corresponding to ages 3–8 yr (Beckman et al. 1990). A mature female with hydrated eggs was observed as small as 625 mmFL; this indicates that size- or age-at-maturity for northern Gulf of Mexico stocks is greater than previously estimated by Simmons & Breuer

Table 3

Effect of location of tissue samples of black drum *Pogonias cromis* for hydrated oocyte counts per unit of ovary weight (g). Locations are anterior (i), mid (ii), and posterior (iii) of ovarian lobes.

	Mean, SE of oocytes/g, and number of tissue samples								
	Right lobe			Left lobe			Both lobes		
Locations	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
i	1714	91	25	1846	170	25	1780	96	50
ii	2025	245	25	2000	199	25	2013	156	50
iii	1944	149	25	1911	180	25	1928	116	50
Total	1895	100	75	1919	105	75			

Two-way ANOVA:

Source of variance	df	SS	MS	F	PR>F
Lobe	1	22490	22490	0.03	0.87
Segment	2	1385533	692767	0.87	0.42
Interaction	2	213348	106674	0.13	0.87
Error	144	14701071	796535		
Total	149	116322441			

(1962) and Pearson (1929) for black drum from Texas waters.

Multiple oocyte stages were present throughout the 1986–87 spawning season, including primary growth (PG), cortical alveolar (CA), and vitellogenic (V) stages. Primary-growth oocytes were present year-round and are a gonadotropin-independent stage (Wallace & Selman 1981, DeVlaming 1983). Oocyte recruitment from this PG population and onset of seasonal oogenesis was signaled by the appearance of CA oocytes in October. Vitellogenic oocytes were noted in November, and both CA and V oocytes persisted until May, indicating the potential for a protracted spawning season.

Descriptions of the breeding season for black drum are varied. Gonad development and possible spawning have been reported during the summer (Pearson 1929, Cornelius 1984 cited in Cody et al. 1985). Our June, July, and October samples did not indicate that spawning was evident. By November, reproductive development for two females (yolk coalescence and final oocyte maturation in histological sections) indicated the potential for spawning to occur. Capture of black drum larvae from offshore Louisiana waters has been reported as early as December (Ditty 1986). Pearson (1929) reported the primary spawning season was February to May. Cody et al. (1985) described seasonality of gonad development of black drum in Texas and reported gravid females during November–April, with spawning or spent stages predominant during February–April. From Florida, Murphy & Taylor (1989) and Peters & McMichael (1990) also report the reproductive season ranges from November to April with February–March spawning peaks.

All the changes noted with the onset, peak, and decline of the spawning season were reflected both in histological samples of ovaries and in gonad weight changes relative to body weight (GSI) for females. Increase in proportion of vitellogenic oocytes was associated with GSI increase in November and December. Appearance of hydrated oocytes and postovulatory follicles in February and March coincided with highest values for GSI. Subsequent appearance of atretic vitellogenic oocytes in April, and increase in atresia in May and June, were associated with declines in gonad weights reflected by decreasing GSI. The GSI seasonal pattern for males coincided with the pattern for females, and suggests a synchrony in development of reproductive states for both sexes. However, mean GSI values must be interpreted with caution. For the same stage of oocyte development, a larger individual may exhibit proportionally larger ovaries and a greater GSI value than a smaller individual (DeVlaming et al. 1982). We apply the GSI here only as a relative measure of changes in reproductive condition over the spawning season, and not as a specific measure of reproductive readiness or histological stage.

Black drum spawn in inside (estuarine, bay) as well as in outside (coastal waters seaward of inlets) waters. Pearson (1929) indicated spawning took place in Gulf waters off Texas, although Simmons & Breuer (1962) presented evidence for spawning in estuaries. Osburn & Matlock (1984) present evidence from tagging studies for a "quasi-permanent" movement of black drum >4 yr from bays to the Gulf, where they may act as spawning stock. Jannke (1971) cited evidence of estuarine spawning in the Florida Everglades, but also indicated that spawning occurred outside the estuarine portion of the park. Peters & McMichael (1990) report that spawning in the Tampa Bay region was likely to have occurred both inside and outside the bay. We also noted spawning activity over a gradient from offshore to inshore. Examination of black drum in hydrated condition from trawl landings during February and March indicated spawning was occurring in coastal waters off Louisiana. During late March, however, females in hydrated condition were taken by haul-seine from inshore estuarine waters east of the Mis-

sissippi River. Drumming behavior associated with spawning was noted in Caminada Pass, Louisiana in April, further documenting inshore reproductive activity (Donald Baltz, Coastal Fish. Inst., LA State Univ., Baton Rouge, pers. commun.).

The dynamic of changing spawning locations may have a seasonal component related to water temperature. Mok & Gilmore (1983) analyzed sound production from black drum in Florida waters and noted "loud drumming," which they associated with spawning, occurring at 18–20°C. They also noted cessation of this drumming during a temperature drop to 13–15°C. Peters & McMichael (1990) provided more direct evidence for onset of spawning at 16–20°C. By correlating seasonal water temperature with larval birthdates, peak births were calculated to have occurred in March when temperatures reached 21–24°C. Although we did not have precise locations and temperatures for commercial catches, our samples of hydrated-oocyte and POF-bearing females indicate that spawning may have predominated in outside waters in February (e.g., trawl landings) and moved to inside waters as seasonal temperatures increased (haul-seine and gillnet landings in March and April). Other factors not examined may influence spawning, including moon phase and tidal period (Peters & McMichael 1990).

Postovulatory follicles probably last longer than 24 h at sea temperatures encountered in coastal Louisiana waters in February and March (19–22°C). Hunter & Macewicz (1985) found POFs for 3–4 d from northern and peruvian anchovies (*Engraulis mordax* and *E. ringens*) spawning at 13–19°C. Based on a higher spawning temperature of 23–24°C, Hunter et al. (1986) found 24 h-old follicles in skipjack tuna that appeared similar to those in northern anchovy held 48 h. Our day-1 POFs appeared similar to 24 h POFs for skipjack tuna shown in Hunter et al. (1986). We estimated black drum follicle duration to be at least 32 h old, due to the presence of recent POFs and older-degenerating POFs together in the same histological sections (i.e., 0–8 h plus 24 h, respectively) which is consistent with spawning on successive nights. If follicles are identifiable well past 24 h, our estimate of average duration between spawning would increase.

Our estimates of spawning frequency, once every 3 or 4 d, are similar to other sciaenid species. Tucker & Faulkner (1987) report a daily spawning fraction of 0.35 (once every 3 d) for captive spotted seatrout. Brown-Peterson et al. (1988) calculated an average daily percentage of wild seatrout in ripe condition to be 27.5% (indicating spawning once every 3.6 d) over a 6 mo reproductive season. Red drum have displayed a spawning fraction of 0.68 (once every 1.5 d) in captivity over a 76 d period (Arnold et al. 1977).

The pattern of appearance of vitellogenic oocytes supports our contention that oocyte recruitment continued during the reproductive season. Therefore, the yolked-oocyte population was not deterministic or representative of annual fecundity (Hunter et al. 1985). Of females examined histologically in February, 73% showed evidence of recent spawning (day-0 females), yet the proportion of vitellogenic oocytes from females did not reach a maximum until March. In contrast, a species with a determinant oocyte development pattern could exhibit multiple spawns but the proportion of vitellogenic oocytes would decrease following onset of spawning (Hunter et al. 1985). With continuous recruitment of batches of oocytes, the traditional method to determine fecundity by enumerating vitellogenic oocytes prior to onset of reproduction (e.g., Bagenal 1968) would underestimate potential fecundity. This method necessitates counting of hydrated eggs just prior to ovulation, i.e., determining batch fecundity and number of spawns in the season (Hunter et al. 1985).

Previously, little fecundity information has been reported for black drum (Sutter et al. 1986). Pearson (1929) estimated fecundity at 6 million eggs for one 110 cm gravid female (107cmFL, 16.4 kg eviscerated weight)* based on extrapolation of wet weight for 60 eggs. Our computation of batch fecundity was 1.6 million eggs for a 6.1 kg female (mean eviscerated weight of 25 females). Figure 4 and comparison with Pearson's result suggest that batch fecundity is a function of body size, but we found this relationship to be quite variable (Fig. 4). While these data do not appear to fit a linear relationship as closely as for smaller sciaenids (DeMartini & Fountain 1981, Brown-Peterson et al. 1988), we only sampled hydrated females measuring 660–876 mmFL. Because females >1000 mm are occasionally landed (e.g., Beckman et al. 1990), a broader range of sizes could illuminate the functional relationship between size and fecundity. Batch size may vary also with the reproductive period and may be higher earlier in the spawning season. Our sample size was too small to detect changes in batch fecundity over the breeding season. However, the pattern of vitellogenesis and GSI provides evidence that spawning peaked in March. The proportion of females in spawning condition was also highest in March. Conover (1985) demonstrated a quadratic batch-fecundity relationship for Atlantic silversides during the breeding season. He postulated that this pattern may occur when optimal

* Calculated from TL-FL regression reported in Murphy & Taylor (1989). The relationship between eviscerated body weight (BW) and fork length (FL) is given by the equation: Ln BW = 2.8835 Ln FL - 10.382 (n=100, r^2=0.964, range 459-1122 mmFL).

conditions for reproduction exist at about the same time each year.

The batch fecundity estimate multiplied by the frequency of spawning provides an estimate of annual fecundity (Hunter & Macewicz 1985, Hunter et al. 1985). For example, annual production could be as high as 32 million eggs for a 6.1kg female with an average clutch of 1.6 million eggs over 20 spawns (assuming spawning every 3 d on average during February and March). Although this estimate of annual fecundity is high for wild fish, spawning patterns in captivity for a closely-related sciaenid, red drum *Sciaenops ocellatus*, corroborates this magnitude of egg production. Three captive female red drum produced 6×10^7 eggs over 76 d, or roughly 20 million eggs/female (Arnold et al. 1977).

Although we found no significant differences in hydrated egg counts between ovarian lobes or among locations within a lobe, we observed the maximum number of hydrated oocytes in the mid-region of ovaries. Hydrated eggs per unit of ovary weight were lowest for the anterior region of the ovary, and may have been due to decreased vascularization or the hydration rate (Hunter et al. 1985, Fitzhugh et al. 1988). In future sampling, we recommend multiple samples be taken for accurate batch-fecundity determinations due to the large ovary size and potential for heterogeneity of hydrated oocytes among locations within the ovary.

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Abstract.—Atlantic menhaden *Brevoortia tyrannus* larvae inflate their swimbladders at night and deflate them during the day. The present study considered the relationship of inflation to light intensity, the time-course of inflation, and the presence of an endogenous rhythm in inflation. The percentage of laboratory-reared larvae that inflate their swimbladders increased upon sudden exposure to a decrease in light intensity. Percentage inflation was maximal at an intensity of 10^{13} photons cm^{-2} s^{-1} and lower. For any specific size of larvae, the inflation volume did not vary significantly with light intensity, but volume increased with total larval length. Inflation began within 5 min of introduction into darkness, and maximum percent inflation was evident by 20 min. There was a rhythm in which darkness induced a low percent inflation during the day phase and a high percentage at the beginning of the dark-phase. This dramatic increase in inflation at sunset may function for predator avoidance.

Swimbladder inflation of the Atlantic menhaden *Brevoortia tyrannus*

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Diel inflation and deflation of the swimbladder are common to larval clupeoid fishes (Uotani 1973, Hunter & Sanchez 1976, Blaxter & Hunter 1982). Both Atlantic (*Brevoortia tyrannus*; Hoss et al. 1989) and gulf (*Brevoortia patronus*; Hoss & Phonlor 1984) menhaden larvae inflate their swimbladders during the night and deflate them during the day. Inflation occurs by moving to the surface, swallowing air into the alimentary canal, and moving it to the swimbladder through the pneumatic duct (Hoss & Phonlor 1984). Deflation is presumed to take place by diffusion, because menhaden have no open connection between the anal opening and swimbladder (Tracy 1920).

Inflation/deflation by menhaden larvae is clearly related to the light: dark cycle. Field studies of both Atlantic and gulf menhaden found most larvae had deflated swimbladders and low swimbladder volumes during the day, with the reverse conditions at night (Hoss & Phonlor 1984, Hoss et al. 1989). Since inflation is rapid, occurring within 1 h after sunset, Hoss et al. (1989) suggested that change in light intensity may cause the inflation response.

The present study was undertaken to determine (1) the relationship between inflation and light intensity for Atlantic menhaden larvae, (2) the time-course for inflation, and (3) the presence or absence of an endogenous rhythm in inflation.

Materials and methods

Atlantic menhaden *Brevoortia tyrannus* were spawned and reared in the laboratory using methods described by Hettler (1983). After egg hatching, the larvae were held in circular tanks (100 L) at about 20°C on a 12:12 h LD cycle. The dark phase began at 1800 h. Lighting during the light phase was provided by daylight fluorescent tubes at a surface intensity of 1.6×10^{15} photons cm^{-2} s^{-1} (400–700 nm) as measured with a scalar irradiance meter with a 4ii collector (Biospherical Instruments, Inc.). Young larvae were fed rotifers *Brachionus plicatilus* cultured in the laboratory. Older fish (13–15 mm) were fed brine shrimp (*Artemia* sp.) nauplii. Larvae measuring 9–20 mm were used in the experiments.

Inflation was quantified by measuring light-refractive bubbles in the swimbladder and alimentary canal to the nearest 0.02 mm under a microscope. It was assumed that any bubbles in the alimentary canal were being transported to the swimbladder. Gas bubble volume was calculated using the equation of Hunter

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& Sanchez (1976): $V = 4/3\ 4ii\ ab^2$, where b = half the bubble width and a = half the bubble length. The total volume of all bubbles was used as the swimbladder volume.

There were three sets of experiments. The first was designed to determine the relationship between light intensity and swimbladder inflation. Larvae were removed from the rearing tanks just before the beginning of the dark phase and maintained under approximately the same light intensity (cool white fluorescent lamps: intensity = 1.7×10^{15} photons cm^{-2} s^{-1}). A control group of the larvae was measured for total length (TL), presence of gas bubbles in the swimbladder and alimentary canal, and size of the bubbles. Similar standard measurements were made on the remaining larvae after being exposed to the test light intensity for 3 h. The light-stimulus source was a 300 W incandescent lamp filtered to the blue region with a Corning 4-96 filter. The transmitted wavelengths encompassed the major spectral-sensitivity maxima of most fish (e.g., Munz 1958, McFarland & Munz 1975). All intensities below the maximum level were controlled by neutral density filters. Each larva was only measured once.

Since the total-length range of larvae was 9–20 mm, an important question is whether all sizes were equally responsive to lighting changes that induce swimbladder inflation. An answer to this question was provided by considering (1) the percentage of different-sized larvae that inflate their swimbladder before and after exposure to new lighting conditions, and (2) the percentage of the total number of larvae sampled in each size-category.

The second set of experiments was designed to determine the time-course for swimbladder inflation. Larvae were again removed from the rearing tank near the end of the light-phase and illuminated at about the intensity used for rearing. Standard measurements were made on a control sample of larvae. The remaining larvae were put into darkness at the beginning of the dark-phase, and standard measurements made on subsamples at various time-intervals (5, 15, 30, 60, 90, 120 min).

The third experiment tested for the presence of an endogenous rhythm in swimbladder inflation. A large group of larvae was removed from the rearing tank at the beginning of the light phase and placed in constant temperature (22°C) and light (cool-white fluorescent lamps: intensity = 1.7×10^{15} photons cm^{-2} s^{-1}) both of which were similar to the light intensity and water temperature of the rearing tanks. Standard measurements were made at 3 h intervals on a subsample of larvae. At the beginning of each of these measurements, a similar subsample was placed in darkness and standard measurements made 2 h later. A change in the percent inflating over the day would suggest the presence of an endogenous rhythm.

The percentage of larvae with inflated swimbladders and the total volume of bubbles in each larva were calculated for each observation within each experiment. Means, standard deviations, and standard errors of percent data were calculated after the data were arcsin-transformed. A Z statistic was used to test differences between two proportions, while a Student's *t*-test was used to compare mean values (Walpole 1974).

Results

Relation of swimbladder inflation to light intensity

The percentage of larvae inflating their swimbladder under all experimental conditions changed with size (Fig. 1). Prior to exposure to new light conditions, the percent of larvae with inflated swimbladders remained relatively low for all sizes of larvae. In contrast, when subjected to a decreased light intensity, the percent response changed dramatically with size. None of the 9 mmTL larvae inflated their swimbladder, and only a low percentage of 10 mmTL larvae showed inflation (Fig 1). Percent inflation increased as size increased, reaching 100% for larvae >17 mmTL. The following study will focus on larvae 11–16 mm in length, because the percent inflation can vary with lighting condition.

Equal numbers of larvae were not sampled in each size-category (Fig. 2), as most larvae were 11–12 mmTL and there were few >15 mmTL. This size distribution

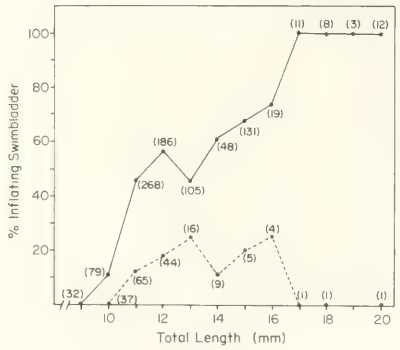

Figure 1

Percentage of larvae inflating their swimbladder versus size for all larvae in the swimbladder inflation versus light intensity experiment (Fig. 3). The dashed line shows the percentages before exposure to different light conditions, and the solid line is the experimental percentages.

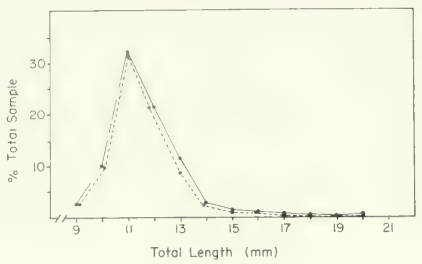

Figure 2

Percentage of the total number of larvae of the different total length sampled for the swimbladder inflation vs. light intensities experiment (Fig 3). Dashed line shows larvae sampled before exposed to different light levels (control; total n=193), whereas the solid line is larvae exposed to different light conditions (experimental; n=834).

was consistent for all experiments. Since the probability of swimbladder inflation was not equal for each size-category (Fig. 1), results will be biased to responses of the most-abundant size if all size-classes are grouped together. Thus, detailed analyses should only consider individual size-classes. The most-abundant size (11 mmTL; Fig. 2) will be used for this purpose.

The percentage of fish inflating their swimbladders increased as they were exposed to lower light intensities (Fig. 3). The highest light intensity to induce a significant increase in the proportion of fish with inflated swimbladders (threshold intensity) varied slightly with fish size. For 11 mmTL larvae (Fig. 3A) the threshold intensity was ~6×10^{13} photons cm^{-2} s^{-1}, whereas for 12–16 mmTL larvae, it was 1 log unit higher (Fig. 3B). For both size-groups, the proportion filling their swimbladders at ~10^{13} photons cm^{-2} s^{-1} and lower light intensities was not significantly different from the proportion in darkness.

The variation in swimbladder volume with light intensity was considered in detail for 11 mmTL larvae (Fig. 4). Mean volume increased as light intensity decreased, but the difference was not significant between the initial mean volume and that in darkness due to large variances (Fig. 4). Similar results were also obtained for 12 and 13 mmTL larvae.

In contrast, swimbladder volume increased proportionately with larvae size (Fig. 5). When the relationship between mean volume (V) in darkness and total length (L) was expressed as the allometric equation ($V=aL^b$), the slope of the regression (b) equaled 5.31 (r^2=0.99, p<0.0001). Means were calculated for larvae of each size in all conditions, because volume did not change with lighting condition (Fig. 4). Since volume changed with larval length, volumes could not be averaged for larvae of different lengths.

Timing of swimbladder inflation

The timing of swimbladder inflation was measured upon transfer from rearing-light intensity to darkness. By producing the maximum rate of intensity change, we assumed the maximum rate of inflation should be evoked. Results were combined for larvae 11–16 mmTL because the proportion inflating in darkness for 11 mm larvae was not statistically different from the proportion of 12–16 mmTL larvae (Fig. 3). A significant increase in the proportion with inflated swimbladders was evident after 5 min in darkness (Fig. 6). The maximum percent inflation was reached within 20 min. The proportion of fish with inflated swimbladders then remained relatively constant for about the next 1.5 h.

Endogenous rhythm in swimbladder inflation

The percent inflating prior to placement in darkness remained low throughout the 24h sampling interval, which

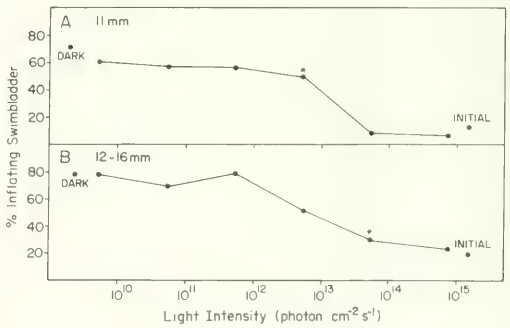

Figure 3

Percentage of larvae 11 mmTL (**A**) and 12–16 mmTL (**B**) inflating their swimbladder when exposed to different light intensities and darkness (dark). "Initial" is the percentage sampled shortly after removal from the rearing tank. Average sample sizes for each condition in A and B are 44 and 58, respectively. Asterisk indicates the highest light intensity to evoke a response that was significantly (p<0.05) greater than the initial response.

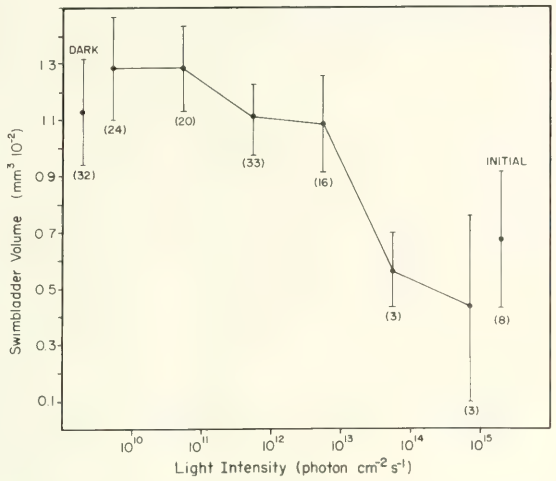

Figure 4

Swimbladder volume of 11 mmTL larvae shortly after removal from the rearing tank (initial) and when exposed to different light levels and darkness (dark). Means and standard errors are shown. Number below each plot is the sample size.

indicates there was no endogenous rhythm in inflation in constant high light conditions (Fig. 7A). Placement in darkness induced inflation in ~40% of the larvae during the normal light-phase. This percentage increased dramatically to 70% at the normal time for the beginning of the dark-phase (Fig. 7A). This response level continued into the time of the next light-phase. Mean swimbladder volume of 11 mmTL larvae varied over time, but the maximum and minimum means over the first solar day were not significantly different due to the large variances (Fig. 7B).

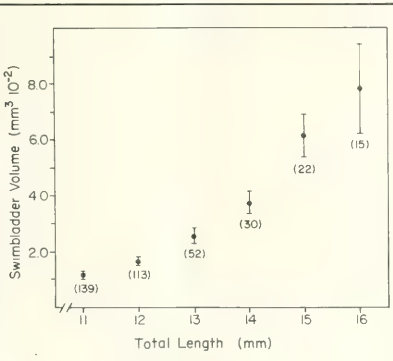

Figure 5

Swimbladder volume vs. total length of larvae from all lighting conditions. Means and standard errors are plotted. Number under each plot is the sample size.

Discussion

Atlantic menhaden inflate their swimbladders in response to a decrease in light intensity. The smallest size observed with an inflated swimbladder was 10 mmTL, which is smaller than the minimum size of 13 mmTL found by Hoss & Blaxter (1982). This difference may result from the large sample size used in the present experiment, since the percentage of 10 mmTL larvae with an inflated swimbladder was ~10%. The percentage of larvae inflating their swimbladder in response to a decrease in light intensity increased with size and reached 100% at 17 mmTL and greater.

Swimbladder volume increased with size, which is not surprising, since larger larvae have larger swimbladders. However, within any fish size, the mean volume did not vary significantly with lighting condition. This result disagrees with the qualitative conclusion of Hoss et al. (1989) and is likely due to the wide variation in volume. Hoss et al. (1989) also found high variances, but failed to compare mean values statistically.

The percentage of larvae inflating their swimbladders increased as the light intensity decreased, which clearly indicates that the decrease in light intensity cued the response. However, a step function was observed, in that once light was below a particular absolute level, maximum inflation occurred. Future experiments are needed to determine whether inflation is cued by exposure to light intensity below an absolute level or to the rate of change in intensity. This information will allow predictions of the time of inflation in the field.

Hoss et al. (1989) failed to find an endogenous rhythm in swimbladder inflation for larvae held under conditions similar to the present experiment. In contrast, our study showed a clear rhythm during the first day for larvae held under constant light. The percent inflation was low in fish introduced to the dark during the time of the light-phase, and nearly doubled at the time the dark-phase began. This high percent response did not return to a low level at the time of the next light-phase. Hoss et al. (1989) did not begin measuring swimbladder inflation until after ~24 h in constant light, which may be why they failed to detect an endog-

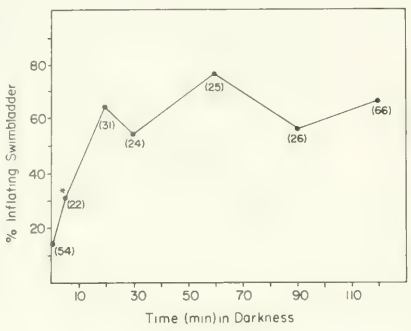

Figure 6

Percentage of larvae 11–16 mmTL filling their swimbladders after different times in darkness. Number under each point is the sample size, and asterisk is the first time that a proportion was significantly greater ($p<0.05$) than the proportion of larvae with inflated swimbladders initially in light, which is plotted at time zero.

enous rhythm. After this time in constant light, variation in inflation after introduction to dark was not evident in the present study. There are two possible explanations for this result. First, the rhythm could fail to continue because larvae were kept in constant light, a condition that frequently suppresses an endogenous rhythm (Hastings et al. 1991). Second, the rhythm could consist of one cycle in which inflation is suppressed during the light-phase and larvae become "ready" to inflate at the beginning of the dark-phase. Readiness then continues until a dark cue is received, which resets the endogenous clock.

Clearly, Atlantic menhaden larvae are adapted for swimbladder inflation at sunset. Their rhythm indicates they are most responsive to a light-intensity decrease at this time and most inflation occurs within 20 min. Such a dramatic response suggests swimbladder inflation has an important functional advantage.

Menhaden larvae are negatively buoyant even with a fully inflated swimbladder. Nevertheless, inflation reduces their sinking rate (Hoss et al. 1989). Past investigators have suggested that swimbladder inflation acts as an energy-saving mechanism, allowing larvae to expend less energy for maintaining their position in the water column at night when they are not feeding (Hunter & Sanchez 1976). During the day, a fully inflated swimbladder may reduce the speed of movement and, thereby, the effectiveness of prey capture and predator avoidance.

In addition, Uotani (1973) proposed that inflation allows larvae to decrease their movement at night, which serves to reduce detection by predators that hunt by vibrations, such as chaetognaths. Field studies show some indication that menhaden larvae undergo reverse diel vertical migration (DVM) in which they descend in the water column near sunset and ascend near sunrise (Hoss et al. 1989). Chaetognaths exhibit the opposite pattern of nocturnal DVM (Pearre 1973, Sweatt & Forward 1985). Reverse DVM is proposed as a mechanism for avoiding zooplankton predators that undergo nocturnal DVM (Ohman et al. 1981, Neill 1990). A slower descent rate at sunset by menhaden larvae due to inflated swimbladders may reduce detection by chaetognaths that are ascending toward the surface. Since the percentage of menhaden larvae with inflated swimbladders increases with size, the importance of reduced sinking rate for predator avoidance may increase with size. The threat of predation to menhaden larvae is probably reduced during their ascent at sunrise because the descending chaetognaths have been feeding all night.

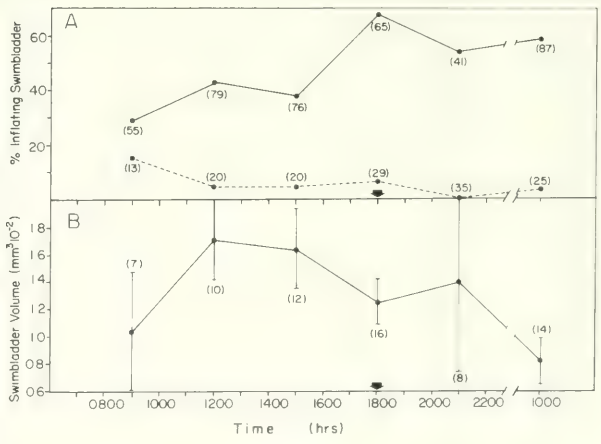

Figure 7

Percentage **(A)** of larvae 11–16 mmTL that filled their swimbladders before (– – –) and after (——) exposure to darkness for 2 h over the solar day. The swimbladder volume of 11 mmTL larvae **(B)** after exposure to darkness is also plotted against time in the solar day. Means and standard errors are plotted. Number near each plot is the sample size. Arrow indicates the times of the beginning of the dark phase of the rearing LD cycle.

Acknowledgments

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Abstract.—Seasonal variability in gonad growth was investigated for the tropical cephalopods *Loligo chinensis* and *Idiosepius pygmaeus*. Statolith ageing techniques enabled a comparison of gonad growth in relation to both individual size and age. Age analyses revealed that male and female individuals of *L. chinensis* matured earlier during the warmer summer period than in the cooler winter period. These preliminary results suggested that maturity was governed more by individual size rather than age. Analysis of seasonal change in the gonadosomatic index (GSI) revealed that *L. chinensis* gonad tissue accounted for the greatest percentage of body weight in the month of October. The trend in the nidamental gland/mantle length index closely paralleled the trend in GSI values for female individuals of *L. chinensis*, while growth of the nidamental gland and hectocotylus closely paralleled growth of the gonad. The seasonal variation in reproductive investment for *Idiosepius pygmaeus* followed a different pattern compared with *L. chinensis*. Slower growing cool-season (spring) individuals lived longer and had comparatively larger gonads than their warm-season (autumn) counterparts, despite no difference in body size between the two seasons. *Idiosepius pygmaeus* thus appeared to be employing a 'trade-off' in its reproductive strategy by partitioning a greater amount of energy into gonad tissue over a longer lifespan during the cooler period of the year.

Seasonal variation in reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small tropical sepioid *Idiosepius pygmaeus*

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In reviewing cephalopod reproduction, Mangold (1987) has emphasised that there are at least as many open questions as there are established facts, and that there are thus many gaps in our knowledge as well as contradictory statements. Recent research (e.g., Hanlon et al. 1989, Rodhouse & Hatfield 1990, Jackson & Choat 1992) is revealing that cephalopod lifespans are considerably shorter than many estimates made over the last several decades. This past confusion has apparently led to a poor understanding of the reproductive tactics of cephalopods. Clearly, any ideas regarding the lifespan of an organism will influence ideas regarding reproductive events in the individual.

Statolith ageing techniques have the potential for resolving some of the discrepancies in our understanding of the reproductive tactics of squids and sepioids. By analyzing individual age and maturity status, age-at-maturity and time-specific schedules of gonad growth can be constructed. The focus of this study was to consider seasonal variation in age-at-maturity and reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small sepioid *Idiosepius pygmaeus*. Statolith ageing techniques have been applied to both *I. pygmaeus* (Jackson 1989) and *L. chinensis* (Jackson 1990a, Jackson & Choat 1992). Analysis of seasonal samples for both of these species has revealed that there was considerable seasonal variation in growth (Jackson & Choat 1992). This study was therefore undertaken to see if there was any seasonal variation in gonad growth or seasonally-induced variation in age-at-maturity in these two species.

Loligo chinensis is common in North Queensland waters and can be captured by bottom trawls throughout all months of the year. The species is sexually dimorphic, with males growing longer than females. In North Queensland waters, males are commonly encountered up to ~180 mm dorsal mantle length (DML), while females are common up to ~120 mmDML. Hatchling size for *L. chinensis* is ~1.4 mm (unpubl. data). In the summer, *L. chinensis* reaches adult size in ~100 d, while winter growth is slower with adult size reached by 140–170 d (Jackson & Choat 1992).

Idiosepius pygmaeus is a common neritic cephalopod which is found in surface waters in mangrove, estuarine, and breakwater habitats (Jackson 1989). This species, however, is only common in nearshore surface waters between March and November, with few specimens observed over the summer months (December–February) (Jackson 1992). *Idiosepius*

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pygmaeus is sexually dimorphic, with females reaching much larger sizes than males. In North Queensland waters, males are commonly encountered up to ~10 mmDML, while females are commonly encountered between 13 and 18 mmDML. Planktonic hatchlings are ~1 mmDML (pers. observ.). This species has a short lifespan, with maturity reached in <80 d (Jackson 1989), and exhibits slower growth during the cooler seasons of the year (Jackson & Choat 1992).

Materials and methods

Loligo chinensis and *I. pygmaeus* were captured from tropical waters off Townsville, North Queensland. Preparation and enumeration of statolith growth increments for both species were similar to techniques used for *Sepioteuthis lessoniana* (Jackson 1990b), although statoliths of *I. pygmaeus* were not ground or polished. Individuals of *L. chinensis* were captured in paired trawl nets (each net had an 11 m gape and 3.8 cm mesh) which were towed for ~20 min. The majority of individuals of *L. chinensis* were captured in Cleveland Bay (19°11'S,146°56'E) in water depth <20 m. Trawling was undertaken generally for one day each month from February 1988 to November 1989, and up to 15 trawls were taken on each sampling date. Individuals of *I. pygmaeus* were captured by dip-netting along a breakwater east of the Townsville harbor (19°15'S,146°50'E; see Jackson 1992). Individuals of *L. chinensis* used in the age analysis were captured on 12 January 1989 (summer, n=37) and 13 July 1989 (winter, n=27). Individuals of *I. pygmaeus* were analyzed from autumn and spring. Individuals (n=41) for the autumn sample were captured during four sampling periods over two years: 22 and 23 March 1988; 21 and 22 March 1989. Individuals (n=38) for the spring sample were from six sampling trips over two months: 10, 23, 24 August 1988; 7, 20, 21 September 1988. The greatest differences in growth rates and population age structure were observed between these two seasonal periods (Jackson & Choat 1992).

Analysis of reproductive structures

Specimens of *L. chinensis* were initially fixed in buffered 10% seawater-formalin to preserve the large tissue mass and later transferred to 70% alcohol to prevent damage to the statoliths. Specimens of *I. pygmaeus* were preserved immediately in 70% alcohol due to their small body size. Gonads were removed, blotted with paper toweling (*L. chinensis*) or filter paper (*I. pygmaeus*), and weighed. Dorsal mantle length (DML) was measured on both species, and nidamental gland length (NGL) and hectocotylus length was measured on female and male individuals of *L. chinensis*, respectively. Measurements were taken with an eyepiece micrometer (*I. pygmaeus*) or with either callipers or a graduated ruler (*L. chinensis*). Maturity was determined by the presence of mature oocytes in the ovary along with large nidamental glands in females, and the presence of spermatophores in males.

To discern the pattern of growth for gonads, the nidamental gland, and the hectocotylus, measurements of gonad weight, nidamental gland length, and hectocotylus length were plotted against both mantle length and age. Due to the large amount of scatter in many of the plots (especially with *I. pygmaeus*) and the complex curvilinear relationship between many of the relationships, regression analyses were not carried out.

Gonadosomatic and NDL/DML indices

The seasonal trend in gonad growth was also examined for *L. chinensis*. Maturity status was determined for 231 individuals from trawl samples between February 1988 and November 1989 (this analysis included data from individuals which were aged from the January 1989 and July 1989 samples). For most samples, all individuals within the adult size-range (>100 mm) were used in the gonad analysis, except for several summer samples in which a very large number of individuals >300 mm were captured.

Parameters measured for each squid were dorsal mantle length, body weight, gonad weight, and nidamental gland length for females. The gonadosomatic index (GSI) was calculated for each specimen as

$$\frac{\text{gonad weight (g)}}{\text{total body weight (g)}} \times 100.$$

For females, the nidamental gland length/dorsal mantle length (NGL/DML) index was also calculated as

$$\frac{\text{nidamental gland length (mm)}}{\text{mantle length (mm)}} \times 100.$$

Analyses of nidamental gland length and hectocotylus length were not carried out for *I. pygnmaeus*.

Results

Loligo chinensis

Gonad growth with age There were differences in the relationship between gonad weight and age for the two samples of *L. chinensis* taken within different seasonal periods (Fig. 1A,B). The relationship between testis weight and age was similar during both sea-

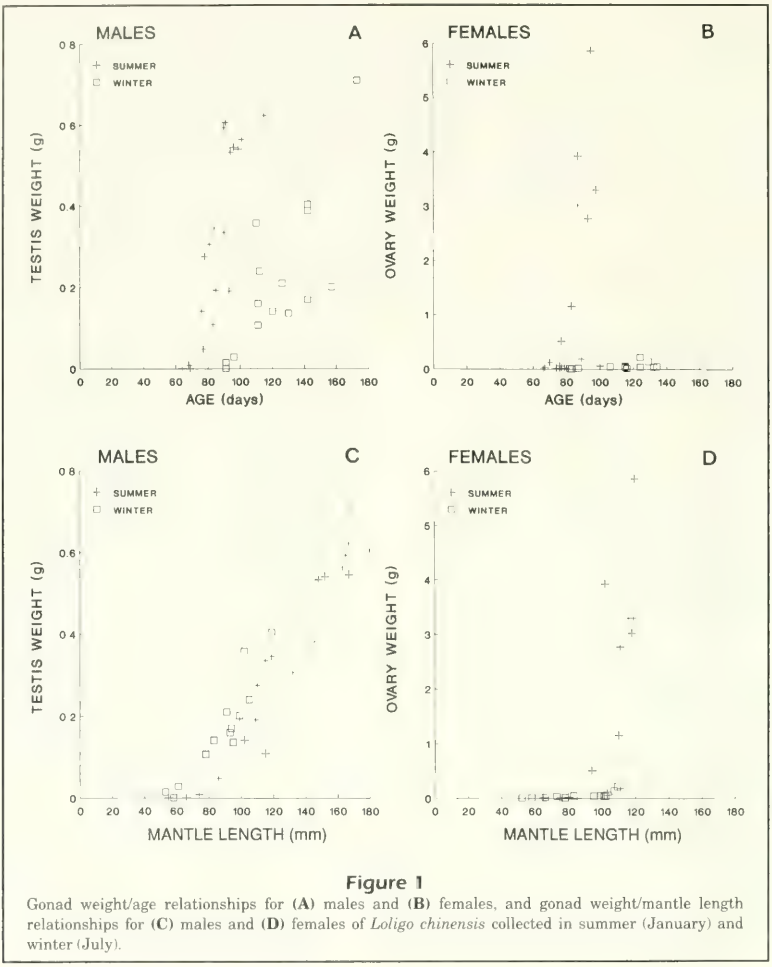

Figure 1

Gonad weight/age relationships for **(A)** males and **(B)** females, and gonad weight/mantle length relationships for **(C)** males and **(D)** females of *Loligo chinensis* collected in summer (January) and winter (July).

sons, with the main difference being the shift in the winter curve to the right (Fig. 1A). Because of seasonally-induced differences in somatic growth (Jackson & Choat 1992), males matured later in winter. The relationship between age and testis weight had greater variability in winter, which suggests that age-at-maturity was less well-defined in the winter, with a slower rate of maturity in some individuals.

In both winter and summer, males with a testis weight >0.1 g had spermatophores present. However, there was variability in age-at-maturity in both seasons, with testis weight in apparent immature males of 0.307–0.335 g. The youngest mature male during summer and winter was 83 d and 111 d, respectively. The oldest immature males for summer and winter were 90 d and 130 d, respectively.

There were also seasonal differences in maturity patterns of females based on ovary weight (Fig. 1B). Females matured in summer at a young age, with the ovary reaching a large size in 65–85 d, although two older specimens were immature. This was especially apparent in the oldest individual (100 d) which also had very undeveloped nidamental glands.

All females in the winter sample had small gonads and nidamental glands, and there were no mature or soon-to-be-mature females. This differed from the pat-

tern observed in males, which had reached maturity in winter, and suggested that female maturity was out of phase with males during this period of the year.

All females aged in summer with an ovary weight >1.161 g were mature, and the ovary filled much of the mantle cavity. The youngest mature female was 83 d, while the oldest immature female was the oldest female aged, 100 d.

Gonad-soma relationships Comparing gonad weight to individual age (Fig. 1A,B) revealed a different pattern than in the gonad weight/mantle length analysis (Fig. 1C,D). Despite the fact that there was a noticeable difference in the testis weight/age scatter plot (Fig. 1A), due to the older winter males, the testis weight/mantle length relationship was similar for both seasons (Fig. 1C). Thus gonad increase was proportional to the squid length rather than its age.

A different pattern emerged when comparing ovary weight/mantle length relationships for female *L. chinensis* (Fig. 1D). Although the lack of maturity was still obvious in winter females, the gonad weight/mantle length relationship for both seasons resulted in a single curvilinear relationship, suggesting that maturity occurred at 100–120 mmDML, regardless of age. Furthermore, although this ageing study indicated that a large proportion of the winter females were older than their summer counterparts, many of the winter immature females were smaller than squids captured in the summer. As with the males, squid size rather than age may be a better indicator of maturity.

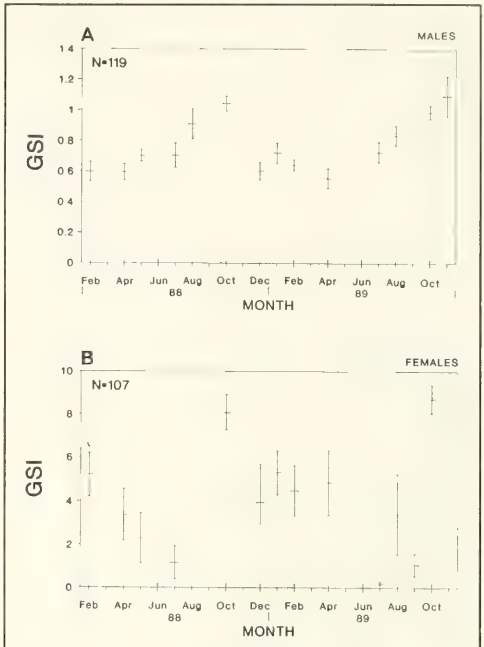

Figure 2
Mean monthly gonadosomatic index for *Loligo chinensis* over the study period for **(A)** males and **(B)** females. Bars = SE.

Reproductive indices Although it was possible to determine the ages of only a small number of individuals in two seasons (n=64), changes in the gonad weight/soma weight relationship throughout the year were examined. For both males and females, a seasonal trend could be detected in the GSI (Fig. 2). In males, GSI values were low, with <1.2% of the total body weight consisting of gonad. In contrast, female GSI values were more variable and generally higher than in males, with the gonad comprising as much as 8% of total body weight.

Mature males were found in all months sampled. However, a regular seasonal oscillation in relative gonad weight was apparent (Fig. 2A). There was an increase in relative gonad weight from April to October in both years. Over the two years, the testis accounted for its greatest percentage (>1%) of body weight in October, while its lowest values were recorded in April.

A similar pattern of fluctuation also existed with the female GSI values (Fig. 2B). In October, females consistently had GSI values that were considerably higher than for other months. Mature females were present in all months except July 1989. As discussed previously, females aged from the 1989 summer sample showed a considerable range in gonad size and level of maturity, despite similarities in both size and age. This range in gonad size was also reflected in the female GSI values, in that the mean values had large standard errors (Fig. 2B) in nearly every month. This was due to the fact that for many months, a proportion of the individuals was immature.

The seasonal trend in the NGL/ML index (Fig. 3) was similar to the trend in the female GSI (Fig. 2B). This index also indicated a greater investment in reproduction during October, with lowest values in July. Furthermore, standard errors were generally less for this index than for the GSI.

The monthly mean mantle lengths for males and females were plotted for the 2 yr period (Fig. 4A,B). Although there was some variation in mantle lengths for the different samples, these could not be related to the seasonal peaks or troughs in the GSI values. For example, the largest females were captured from February to July 1988 (Fig. 4B). However, GSI values dropped considerably over this period. Furthermore, mean mantle length was not highest in October for

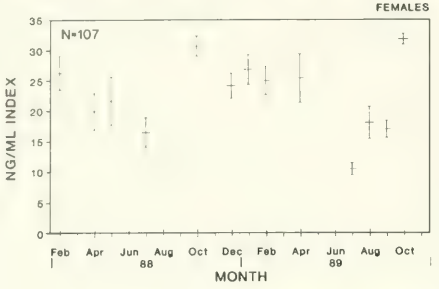

Figure 3

Mean monthly index of nidamental gland/mantle length for female *Loligo chinensis* collected over the study period. Bars = SE.

each year, and although 1989 July values were slightly lower than the other months, the July 1988 values were not. The observed changes in relative gonad weight can thus be considered unbiased by individual size.

Nidamental gland and hectocotylus lengths Nidamental gland length was perhaps the most useful measurement in female squids for obtaining an index of maturity. The relationship of nidamental gland length to mantle length and age of female specimens of *L. chinensis* (Fig. 5) closely resembled the ovary weight/age and mantle length relationships for this species (Fig. 1B,D). For example, two separate relationships were apparent when nidamental gland length was plotted against age, whereas both seasons' data points produced one curvilinear relationship for nidamental gland length vs. mantle length. As with the ovary data, these data suggest that nidamental gland length was more closely related to mantle length than to age.

Similarly for males, hectocotylus length vs. mantle length and age (Fig. 6) exhibited the same pattern observed in the testis weight/age and mantle length relationships (Fig. 1A,C). For example, in winter there was a shift along the age axis, producing a separate correlation for the summer hectocotylus length/age data. However, there was some indication that at large sizes, faster-growing (summer) males had a shorter hectocotylus than slower-growing (winter) males. This relationship was similar to the testis weight/mantle length relationships for *I. pygmaeus* (Fig. 7C,D) seen below.

Idiosepius pygmaeus

Gonad growth with age In contrast to *L. chinensis*, within-season variability in maturity and age-specific

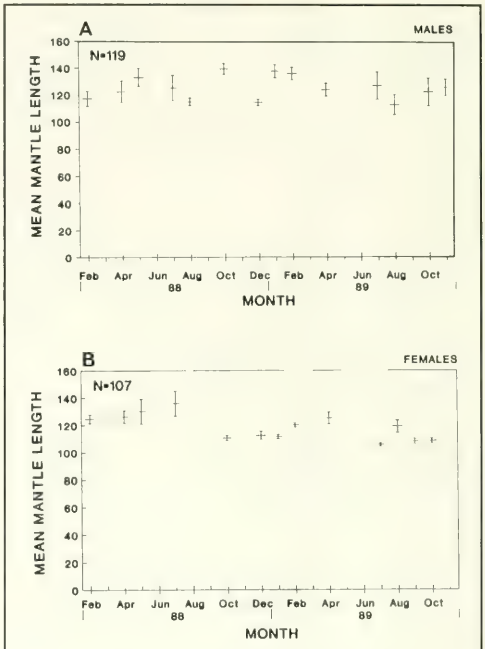

Figure 4

Mean monthly mantle length for **(A)** males and **(B)** females of *Loligo chinensis* used in gonad weight analysis and nidamental gland length analysis (Figs. 2,3).

trends for *I. pygmaeus* could be determined with a greater degree of accuracy. This was possible because of the greater number of replicate sub-amples taken during each seasonal period (see Methods).

The seasonal pattern of gonad growth was different for *I. pygmaeus* than for *L. chinensis*. The seasonal influence on gonad growth and maturation may have been somewhat less for individuals of *I. pygmaeus* (analyzed for spring and autumn) compared with individuals of *L. chinensis* (analyzed for summer and winter). However, individuals captured in autumn would have grown over the warmer period at the end of summer, while individuals from the spring sample would have grown and matured through the colder period, at the end of winter.

Due to the considerable scatter in age/length relationships for this species (Jackson & Choat 1992), there was also considerable scatter in the gonad weight/age relationship (Fig.7A,B). While gonad weight/age relationships for *L. chinensis* resulted in different scatter plots separated on the age continuum (x axis), the pattern was modified differently for *I. pygmaeus* for

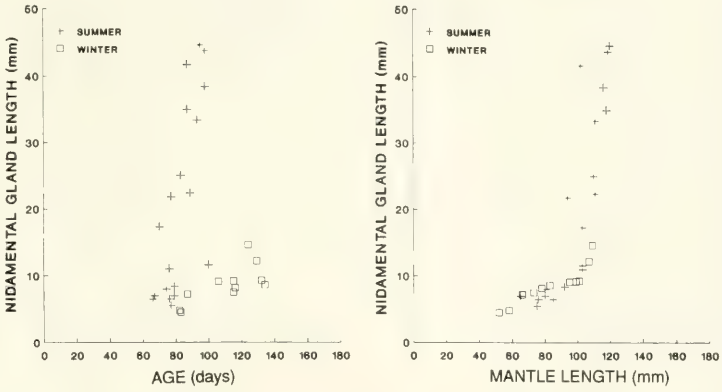

Figure 5

Nidamental gland length/age relationships and nidamental gland length/mantle length relationships for female individuals of *Loligo chinensis* collected during summer (January) and winter (July).

the two seasons (i.e., both seasons' data points fell within the same scatter plot). While individuals of *I. pygmaeus* were older in the spring samples, their gonads reached a proportionally greater weight than did the autumn individuals.

Males The relationship for testis weight vs. age (Fig. 7A) was the same for both seasons, with data points clustering on a single testis weight/age continuum, with the exception of one 41 d individual which fell considerably outside the cluster of data points. The major difference in the seasonal component of the data was a clustering of data points for each season at opposite ends of the testis weight/age continuum, with spring individuals reaching a greater age and possessing proportionally heavier testes than their autumn counterparts.

The youngest mature males in spring and autumn were 22 d and 37 d, respectively, while the oldest im-

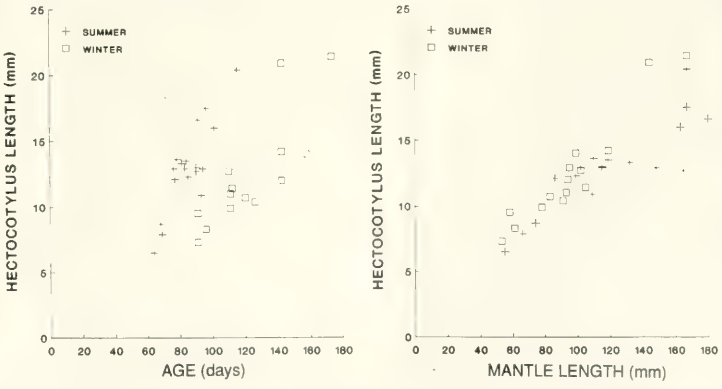

Figure 6

Hectocotylus length/age relationships and hectocotylus length/mantle length relationships for male individuals of *Loligo chinensis* collected during summer (January) and winter (July).

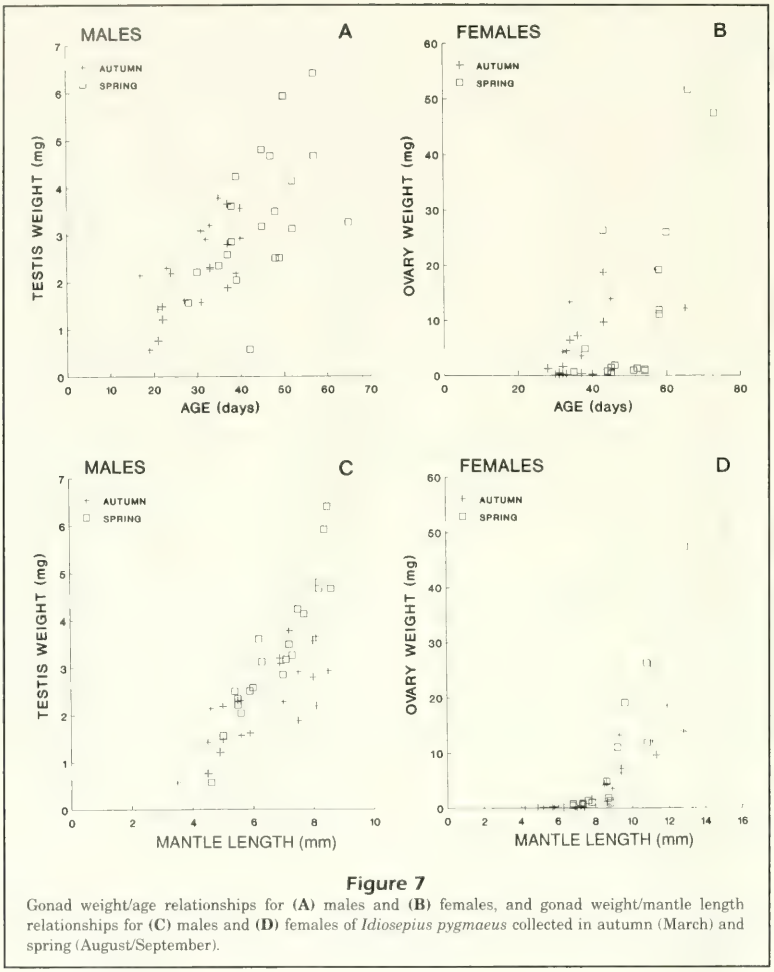

Figure 7

Gonad weight/age relationships for **(A)** males and **(B)** females, and gonad weight/mantle length relationships for **(C)** males and **(D)** females of *Idiosepius pygmaeus* collected in autumn (March) and spring (August/September).

mature males for both seasons were 32 d and 38 d, respectively.

Females A similar relationship to the males also existed in the ovary weight/age relationship, i.e., both seasons' data points tended to cluster along one ovary weight/age continuum (Fig. 7B). However, the scatter was greater than for males, due to the fact that in both seasons there were individuals with very small ovaries. For example, in both seasons, individuals of 40–60 d showed a considerable range in ovary weight. However, as with male testis weight, the spring females also had the heaviest ovaries. Although a number of females had large well-developed ovaries, none of the specimens examined had any mature ova present.

Gonad-soma relationships One possibility for the greater gonad weight in spring vs. autumn could have been due to larger individuals being captured in the spring. However, the plot of gonad weight against mantle length for both sexes (Fig. 7C,D) revealed no size difference in males between seasons and only one spring female slightly larger than the other females. Although there is some overlap in the data for the smaller individuals for both seasons, in the larger sizes,

slower-growing spring individuals did, in fact, eventually produce larger gonads than their autumn counterparts.

Discussion

The biotic and abiotic influences on maturity are complex. Factors such as light (day length), temperature, and food availability can all affect rate and age-at-maturity. Gonad development is directly under hormonal control, and appears to be influenced by the optic gland (Mangold 1987, Boyle 1990). However, the process of maturity is not completely understood and may also be controlled to a certain degree by individual genetic factors, apart from outside influences (Mangold 1983). This study gives preliminary insight into the maturation process in tropical squids and sepioids based on age information. Statolith ageing techniques should prove useful in providing a timescale on the squid maturation process and problems encountered with variation in size-at-maturity.

Loligo chinensis

Variability in size-at-maturity appears to be a common phenomenon with cephalopods. Hixon (1980) found that some immature *Lolliguncula brevis* females were as large as other fully-mature individuals. Considerable variation in maturity has also been shown to exist in *L. opalescens*, with females maturing by 81 mmDML while other females remain immature until 140 mmDML (Hixon 1983). Similar discrepancies in size-at-maturity have also been documented for *Sepia officinalis* (Boletzky 1983) and *Dosidicus gigas* (Nesis 1983). Mangold (1983) has also demonstrated that cultured octopuses reared from the same egg mass reached maturity independent of sibling size or age. The delay in maturity for some *L. chinensis* females for a given length (e.g., Fig. 1B, summer) is similar to observations made for *Lolliguncula brevis* by Hixon (1980). However, in contrast to the other studies cited above, *L. chinensis* females do not show a wide difference in size-at-maturity. The fact that maturity was more closely related to length than to age suggests that there might be some physical or physiological mechanisms controlling maturation apart from age. Some female cephalopods have been shown to develop eggs only when a minimum threshold in body size is achieved (Mangold 1987). The maximum size for individuals of *L. chinensis* obtained in this study is smaller than the maximum size recorded for the species, which is up to 300 mmDML (Roper et al. 1984). This suggests that the squids in Cleveland Bay may be a precocious population which is maturing near the minimum threshold in body size for the species. This could therefore account for the restricted size-range at maturity.

Although male and female *L. chinensis* were mature in the same age-range in summer, a different situation existed in winter, suggesting that maturity in the female winter population was out of phase with the males. This situation has been noted with *Todarodes pacificus* in which males reach maturity 3–6 mo earlier than females (Okutani 1983). This may not be an ecological constraint, considering the reproductive tactics of cephalopods. In many species of cephalopods, males mate with immature females (Mangold 1987) with the females retaining the spermatophores until they spawn. An extended interval between mating and spawning has also been noted in octopods, with up to a 114 d interval between spermatophore transfer and spawning (Boyle 1990).

Alternatively, the apparent absence of mature females in July may have been due to inadequate sampling, since the oldest-aged female captured in winter was 134 d whereas males as old as 173 d were captured. Since maturation was rapid (e.g., females matured in <80 d in summer), it is possible that older mature females existed in winter but that none were captured.

Based on previous work on the effect of temperature on growth rate (e.g., Forsythe & Hanlon 1988 and 1989), seasonal differences in water temperature may also account for the lack of gonad development in *L. chinensis* during winter. As age of field specimens in relation to maturity processes has not previously been considered, only aquarium culture experiments are available for comparison. Richard (1966, cited in Mangold 1987) has shown that males and females of the cuttlefish *Sepia officinalis* from the English Channel, which were raised at 20°C, attained sexual maturity at 7 mo and 140 mmDML, while conspecifics raised at 10°C were totally immature at the same age and were only 50 mm in length. Moreover, Richard (1970, cited in Mangold 1987) also found that females of *S. officinalis* raised at 18°C had a gonad index of 8% at 270 d, while it took 480 d for females raised at 13°C to reach the same value. Other factors, such as seasonal variability in food supply and day length may also influence seasonal differences in maturation rates.

The fluctuations of the GSI and NGL/ML index indicated that ambient environmental conditions (e.g., temperature and food availability) were influencing both the maturity process and the energy *L. chinensis* partitioned into reproduction. Although individuals were often mature (e.g., the majority of males analyzed) there were time-periods when the ovary and testes accounted for a greater percentage of total body weight. This was consistently recorded for both sexes

in the month of October, and would coincide with the spring warming of water in Cleveland Bay after low winter temperatures which begin to rise in August/September (Kenny 1974, Walker 1981). Highest GSI values were also reported for male and female *L. vulgaris* during the spring period in the Mediterranean (Worms 1983).

The interpretation of fluctuations in the GSI and NGL/DML index is complex due to a variety of factors: (1) *L. chinensis* exhibits fast growth and has a short lifespan, therefore annual data sets reflect a number of different generations of squids; (2) because of rapid growth and the observed variability in gonad growth (especially in females), greater sample numbers would be needed to adequately describe gonad growth fluctuations on a smaller scale (e.g., intramonthly variability); (3) due to the tropical nature of the environment, squids (especially males) are mature throughout most months of the year and, therefore, gonad indices are generally reflecting periods of greater investment in reproductive structures rather than periods of immaturity vs. maturity.

The data peaks in October may have been due to the increasing day length in spring, stimulating the optic gland to produce increased hormonal levels which accelerates gonad growth (see Mangold 1987). Since day length would be shortened over the winter period (June–August), the increasing day length during the spring period, along with increasing water temperatures, may produce physiological responses leading to maximal gonad growth. More intensive sampling (e.g., fortnightly) over the late-spring and early-summer period may provide a clearer picture of relative gonad growth over this period. The relationship between mantle length and NGL could constitute a good maturity index for females, since the relationship between NGL and DML is closer than the relationship between DML and gonad weight (Worms 1983). Data for females of *L. chinensis* from this study suggest that the NGL/DML index provides results very similar to GSI values. Maturity parameters based on NGL alone could constitute a more convenient means to determine maturity for tropical squids.

Nidamental gland length The fact that length of the nidamental gland of *L. chinensis* bears a very close resemblance to growth of the gonad highlights the close association this organ has with maturation and egg development. The nidamental gland serves the function of producing a gelatinous matrix which encases the cephalopod egg (Roper et al. 1984). Previous studies have used the NGL/DML ratio as a convenient means to assess maturity. Temperate loliginids have been shown to possess mature oocytes when this ratio is >0.2 (Yang et al. 1986, Hanlon et al. 1989). This relationship generally holds well for females of *L. chinensis*. Out of 112 females (captured throughout the 2 yr sampling period) analyzed for this ratio, all the mature females had an NGL/DML ratio >0.2. Of the immature females analyzed, six individuals (5.4%) had a ratio >0.2 (highest value=0.26). This parameter therefore appears to be useful for tropical loliginids as well. The 0.2 NGL/DML ratio does appear to be the minimum parameter for mature females.

Nidamental gland measurements are thus useful for providing a rapid and convenient means of assessing the level of maturity in tropical loliginids. The nidamental gland can also provide useful information about the past history of a female squid. The fact that some of the larger, older, immature females captured during January had small underdeveloped nidamental glands was one means to ascertain that these females had actually not yet matured and had not regressed from a previously mature condition.

Hectocotylus length The hectocotylus is an important reproductive structure employed by the male to pass spermatophores to the female during copulation. It is also extremely useful for quick sexual identification of preserved specimens. Coelho et al. (1985) carried out a detailed study of the growth of the hectocotylus of *Illex illecebrosus* to determine if the degree of hectocotylization of the fourth arm could be related to maturity. However, no close relationship was found between maturity and the degree of hectocotylization. A partial explanation for this lack of relationship between these parameters was attributed to the fact that the squids examined might have included individuals which hatched at different localities and which had developed under different temperature regimes (e.g., some squids could have been immigrants from a more southerly population exposed to warmer temperatures). This could well account for considerable confusion in the *Illex* data, as individuals of *L. chinensis* from different seasons showed a different relationship between hectocotylus length and mantle length, and hectocotylus length and age. These seasonal growth patterns which were temperature-related did have an influence on the development rate of the hectocotylus, with slower-growing individuals eventually possessing a larger hectocotylus than their faster-growing counterparts. Different-sized hectocotili on similar-sized squids could therefore indicate that the squids had developed under different growth rates. This also suggests that the size ratio of many other structures to body size may also be influenced by the ambient temperature in which the squid develops. Parameter ratios and indices used for taxonomic purposes should therefore be cautiously employed, at least for nearshore squids, and, whenever possible, parameters should be measured in

individuals captured under similar environmental conditions.

Idiosepius pygmaeus

The pattern of gonad maturation in tropical squids and sepioids becomes more complex when the pattern of seasonal maturation of *I. pygmaeus* is also considered. As with *L. chinensis*, individuals of *I. pygmaeus* which grew during a cooler time of the year also reached a greater age. However, gonad maturation was modified in a different way compared with *L. chinensis*. For example, in both seasons males (including mature individuals) had similar-sized testes at an age of 30–40 d suggesting that a minimal gonad size can be reached in just over a month. Nevertheless, as the cooler-season males continued to grow, the gonad continued to reach an appreciably greater size, for the same-sized individual. Thus, environmental constraints (such as temperature, food availability, or light levels) produced a different allometric gonad-soma relationship in this species which was not apparent in *L. chinensis*.

The fact that *I. pygmaeus* has a short lifespan and rapid growth may account for the lack of females with mature ova. It is possible that ovum maturation could take place very rapidly just before egg deposition. Therefore, it could be difficult to capture females with mature oocytes unless it was just prior to egg deposition. Alternatively, females with ripe ova may not have been near the water surface and therefore not available for sampling.

Idiosepius pygmaeus appears to be employing a 'trade-off' in its seasonal reproductive tactics, that is, benefiting from one process bought at the expense of another (Begon et al. 1986). During the cooler period of the year, growth is slowed (presumably as a result of metabolic responses to temperature), therefore lifespan is increased as a necessity, since individuals take longer to reach adult size. As a result, *I. pygmaeus* appears to change its tactics by partitioning a greater amount of energy into gonads over the longer lifespan. Although a longer time-period is taken to reach maturity, there would be a reproductive advantage in that possessing larger gonads would increase reproductive output. A similar situation has been shown to exist with teleost fishes. Stearns (1976) has provided evidence from several species of teleosts, showing that the ratio of ovary weight to body weight (as a measure of reproductive effort) increased with age.

The fact that this phenomenon occurs in *I. pygmaeus* and not the larger *L. chinensis* may be due to the need for *I. pygmaeus* to maximize its reproductive chances because of the greater nearshore habitat variability, or because of the greater constraints this species faces due to its small body size.

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Abstract.—Recent papers have provided new insights into the problem of estimating von Bertalanffy growth parameters from tag-recapture data. In particular, the inconsistency and bias of Fabens' (1965) estimates appear to have been addressed by James (1991). Using simulation, we examine the pattern of bias associated with different error assumptions for Fabens' estimates, weighted Fabens' estimates proposed by James, and a robust method also proposed by James. Our results corroborate James' finding that his robust estimates can be significantly less biased than other methods. We then apply these estimators to tag-recapture data obtained for sablefish *Anoplopoma fimbria* found in the Gulf of Alaska and off the U.S. west coast, and Pacific cod *Gadus macrocephalus* found in the eastern Bering Sea. These species are difficult to directly age, so tag-recapture data provide welcomed independent estimates of growth parameters and an indirect method of validating age-determination criteria. The von Bertalanffy parameter estimates using tag-recapture data and James' method were most similar to estimates calculated directly from length-at-age data.

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Estimating von Bertalanffy growth parameters of sablefish *Anoplopoma fimbria* and Pacific cod *Gadus macrocephalus* using tag-recapture data

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In its most common form, the von Bertalanffy growth curve has three parameters (L_∞, K, t_0). Conventional interpretation of these parameters is that L_∞ is asymptotic size, K describes the growth rate, and t_0 describes the age at length-0. Fabens (1965) was apparently the first to show how least-squares could be used to estimate two of these parameters (L_∞, K) from tag-recapture data. If at least one additional value of length-at-age was known, then t_0 could be estimated, and hence all values of length-at-age could be estimated directly from recapture data without recourse to direct ages from individual specimens. Besides providing growth-curve estimates, such a procedure would seem to provide an indirect validation of ageing criteria, since estimated growth parameters from length-at-age data and tag-recapture data could be compared.

However, comparisons of growth curves estimated using Fabens' method and ordinary length-at-age data seemed to provide evidence that Fabens' method provided biased parameter estimates. Following the suggestion of Chapman (1961) and others, Sainsbury (1980) showed how individual variability [i.e., the possibility that each fish has different values of (L_∞, K)], could lead to bias in population parameter estimates. Francis (1988a) argued from a sampling point of view that von Bertalanffy parameters calculated from length-at-age and tag-recapture data could be different. He also argued that average growth parameters for individual fish may not describe the population growth curve (Francis 1988b). Maller & deBoer (1988) showed mathematically and with simulation that Fabens' estimates, and related estimates of Kirkwood & Somers (1984), could be inconsistent. Kirkwood (1983) suggested combining length-at-age and tag-recapture data into a single likelihood model, but did not address the problem of bias caused by the interpretation of tag-recapture data.

A recent paper by James (1991) suggests that bias in Fabens' estimates could arise from bias in the estimating functions. James shows how weighted least-squares can be used to derive improved estimates for Fabens' method under the usual "observational error" assumption. James also gives distribution-free estimates for a more general model in which, in addition to the usual observational error, L_∞ itself is allowed to vary among individual fish. Although James' estimates appear to be consistent and less biased than the least-squares estimates, they also appear to be less efficient, usually

having larger standard errors. Nevertheless, James' method provides us with more robust parameter estimates.

This paper illustrates how critical is statistical methodology to the estimation of growth parameters from tag-recapture data. We show, by simulation and through analysis of actual data, that different estimation methods can easily lead to very different parameter estimates. With the help of simulation, we feel that realistic choices can be made among these estimators. For the actual datasets chosen for this paper, we are able to compare growth-curve parameter estimates from tag-recapture data with parameter estimates calculated from length-at-age data, using ages estimated from directly counting annuli. This provides another criterion for choosing among estimators.

Methods

We apply estimators considered by James (1991). The "unweighted Fabens" estimates (Fabens 1965) is the widely used historical method. What we call the "weighted Fabens" estimates, and James' estimates, were derived by James (1991). The weighted Fabens' method weights the residuals by an inverse variance estimate and appears to work well for the observational error model. James' estimators appear to be less prone to bias than the unweighted Fabens' estimators, and more robust to the presence of variability in L_∞ than the weighted Fabens' estimators. A more theoretical description of these estimators can be found in James (1991).

First we present a simulation study that corroborates the main findings of James (1991). Our study is more systematic than that of James (1991), using three estimation methods and error structures and calculating mean square error. Our simulation is based on parameters estimated for a marine teleost, Pacific whiting *Merluccius productus*, while James' simulations dealt with two shellfish species. Nevertheless, these simulations should be considered an addendum to James' original work.

Using notation similar to James (1991), consider a population having von Bertalanffy parameters (L_0, K_0) which we wish to estimate. L_0 refers to the average value of L_∞ in the population, where L_∞ might vary among individual fish. We assume $K=K_0$ does not vary among fish. Also, recall that t_0 cannot be estimated from tag-recapture data alone. To determine t_0 we need the average length of at least one age-group which can be supplied by direct age data (i.e., ages obtained from directly counting annuli), or the modal length-frequency of a dominant year-class of known age.

Suppose we observe the size at release (y_{1i}) and recapture (y_{2i}) of i=1,...,n fish, and the ages at release and recapture are (t_i, t_i+d_i). Suppose also that independent normally-distributed errors (ε_{1i}, ε_{2i}, ε_{3i}) enter into these observations in three possible ways:

$$y_{1i} = (L_0 + \varepsilon_{3i})[1.0 - \exp(-K_0 t_i)] + \varepsilon_{1i}$$

$$y_{2i} = (L_0 + \varepsilon_{3i})[1.0 - \exp(-K_0(t_i + d_i))] + \varepsilon_{2i}.$$

We refer to ε_{1i} and ε_{2i} as "observational errors" and ε_{3i} as "variability in L_∞."

The three estimators of (L_0, K_0) considered in this paper are all based on the "residuals":

$$\eta_i = y_{2i} - y_{1i} - (L_0 - y_{1i})[1.0 - \exp(-K_0 d_i)].$$

These estimators are:

1 Unweighted Fabens, estimated by minimizing $\Sigma\eta_i^2$
2 Weighted Fabens, estimated by minimizing $\Sigma\,[\eta_i^2/(1.0+\exp(-2K_0 d_i))]$.
3 James, estimated by solving the simultaneous equations $\Sigma\eta_i=0$ and $\Sigma d_i\eta_i=0$.

Unweighted and weighted Fabens' estimates, and their standard errors, were calculated using nonlinear least-squares methods. Define $g_1=\Sigma\eta_i$ and $g_2=\Sigma d_i\eta_i$. James' estimates were calculated as suggested by James (1991) by solving for "L_0 in terms of K_0 from g_1 followed by substitution into g_2" and then applying the bisection method to estimate K_0 (see Press et al. 1986). This method appeared computationally robust and suitable for simulation studies. The variance estimates of these parameter estimates were calculated according to James (1991):

$$\mathrm{cov}(\hat{L},\hat{K}) = G^{-1}D(G')^{-1},$$

where

$$G = \begin{pmatrix} \frac{\partial g_1}{\partial K_0} & \frac{\partial g_1}{\partial L_0} \\ \frac{\partial g_2}{\partial K_0} & \frac{\partial g_2}{\partial L_0} \end{pmatrix}, \qquad D = \Sigma\eta_i^2 \begin{pmatrix} 1.0 & d_i \\ d_i & d_i^2 \end{pmatrix},$$

and the right-hand expressions are evaluated at the estimated parameters.

Our simulation considered three different error assumptions.

Simulation 1 The observational error model where all fish are assumed to have common growth parameters, with variation due wholly to observational errors ε_{1i}, $\varepsilon_{2i} \sim N(0,\sigma^2)$. Here, all ε_{3i} are assumed to be zero.

Simulation 2 The variation in L_∞ model, where all variation in the observations are due to $\varepsilon_{3i} \sim N(0,\sigma^2)$,

and all observational errors ϵ_{1i} and ϵ_{2i} are assumed to be zero.

Simulation 3 Both observational errors and variation in L_∞ are present in this model, with ε_{1i}, ε_{2i}, $\varepsilon_{3i} \sim N(0,\sigma^2)$.

For these simulations, we assume that the true population parameters are (L_0= 61.23, K_0=0.296), parameters previously estimated for female Pacific whiting (Kimura 1980). Measured in years, t_{1i} and d_i were uniformly and independently distributed over the interval [1, 5], assuming 365 d/yr. New values for t_{1i} and d_i were generated for every replication of the simulation.

Analytic standard errors of parameter estimates were estimated using nonlinear least-squares methods, and the variance estimate described above for James' method. In addition, the sample standard errors (i.e., the sample standard deviation of the replicate parameter estimates) are also provided. The reason for this is that the simulations included variation in t_{1i} and d_i that would not be included in the analytic estimates of standard error, and the probability that the analytic standard errors are themselves biased due to failure of assumptions. For the actual datasets, analytic standard errors were used. For simultaneously considering bias and variance, we include estimates of mean square error (MSE) calculated in the usual way: $\Sigma(\text{estimate} - \text{true})^2/n$.

Following a presentation of simulation results, we analyze tag-recapture data collected for sablefish *Anoplopoma fimbria* from the Gulf of Alaska and off the U.S. west coast, and Pacific cod *Gadus macrocephalus* from the eastern Bering Sea (Fig. 1). Because sablefish and Pacific cod are difficult species to directly age, their growth-curve parameters estimated from tag-recapture data are of special interest. The von Bertalanffy parameters estimated from tag-recapture data were compared with parameters estimated from length-at-age data based on direct ages (i.e., ages from directly counting annuli). For sablefish, we use length-at-age datasets based on break and burn ages (Chilton & Beamish 1982) and parameters estimated using nonlinear least-squares (Kimura 1980). For Pacific cod, we compare tag-recapture results with published von Bertalanffy parameter estimates (Thompson & Bakkala 1990).

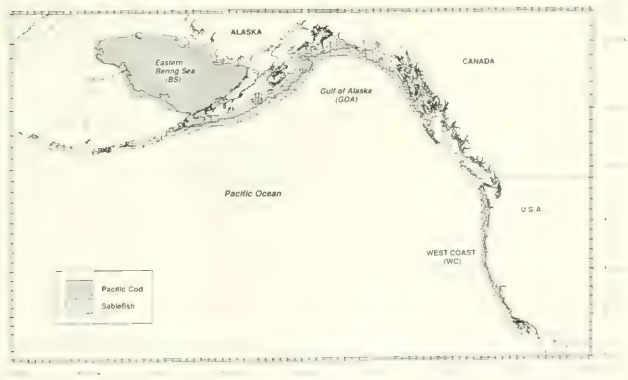

Figure 1
Tag and recovery areas for Pacific cod in eastern Bering Sea **(BS)**, sablefish in Gulf of Alaska **(GOA)**, and sablefish off U.S. west coast **(WC)**.

Results

Simulation results

For the simulation results given here, the tag-recapture sample size was n=300, simulations were replicated 200 times, and the normal errors (ε_{1i}, ε_{2i}, ε_{3i}) were all independently distributed with σ^2=25. Therefore, the sample size was realistically small and the error variances were substantial. For each estimation method and parameter, simulation results (Table 1) were summarized by four entries: sample mean of the estimated parameter, mean analytic standard error, sample standard error (i.e., the standard deviation of estimated parameters), and mean square error.

The unweighted Fabens' estimate of L_0 is biased low in Simulation 1, biased high in Simulation 2, with biases apparently canceling each other in Simulation 3. For the weighted Fabens' estimates, the L_0 estimate is unbiased for Simulation 1, but biased high for Simulations 2 and 3. James' estimate of L_0 is unbiased in Simulation 2, and only modestly biased in Simulations 1 and 3. Biases in L_0 and K_0 estimates are in the opposite direction, as might be expected from the negative correlation between these parameter estimates.

Standard errors are uniformly smallest for the unweighted Fabens' method, in the middle for the weighted Fabens' method, and largest for James' method.

Performance as measured by mean square error was entirely dependent on the assumptions of the simulation. For Simulation 1 (i.e., observational errors) the weighted Fabens' method MSE was smallest; for Simulation 2

Table 1

Simulation results using three different methods to estimate von Bertalanffy parameters (L_0=61.23, K_0=0.296) under three different error assumptions: Simulation 1 (observational error), Simulation 2 (variation in L_∞), and Simulation 3 (both observational error and variability in L_∞). For each estimation method and parameter, simulation results are summarized by four entries: sample mean of the estimated parameter, mean analytic standard error, sample standard error (i.e., standard deviation of estimated parameters), and mean square error.

Method	Parameter	Sim. 1	Sim. 2	Sim. 3
Unweighted	mean(L_0)	58.00	65.01	60.39
Fabens	mean(K_0)	0.379	0.238	0.315
	analytic SE(L_0)	1.042	0.981	1.423
	analytic SE(K_0)	0.031	0.011	0.028
	sample SE(L_0)	0.987	0.991	1.370
	sample SE(K_0)	0.030	0.012	0.026
	MSE(L_0)	11.426	15.272	2.576
	MSE(K_0)	0.00775	0.00347	0.00103
Weighted	mean(L_0)	61.24	67.05	67.21
Fabens	mean(K_0)	0.298	0.215	0.216
	analytic SE(L_0)	1.355	1.154	2.347
	analytic SE(K_0)	0.021	0.009	0.018
	sample SE(L_0)	1.542	1.205	2.921
	sample SE(K_0)	0.030	0.012	0.027
	MSE(L_0)	2.365	35.347	44.197
	MSE(K_0)	0.00091	0.00671	0.00714
James	mean (L_0)	62.22	61.23	62.06
	mean (K_0)	0.294	0.299	0.300
	analytic SE(L_0)	4.099	1.588	4.625
	analytic SE(K_0)	0.064	0.028	0.071
	sample SE(L_0)	4.241	1.521	5.332
	sample SE(K_0)	0.066	0.027	0.069
	MSE(L_0)	18.871	2.303	28.986
	MSE(K_0)	0.00432	0.00072	0.00471

(variability in L_∞) the James' method MSE was the smallest; for Simulation 3 (i.e., both observational error and variability in L_∞) the unweighted Fabens' method MSE was the smallest.

It is clear from these simulation results that unweighted or weighted Fabens' estimates of von Bertalanffy parameters can be significantly biased. It is also clear that standard errors for James' estimators tend to be larger than standard errors for the unweighted and weighted Fabens' estimators.

Estimates from sablefish tag-recapture data

Sablefish is a species characterized by rapid growth at young ages followed by extremely slow growth at older ages. In tag-recapture data, it is common for sablefish to show negative growth increments (Figs. 2,3,5,6). The exact reason for this apparent shrinkage is uncertain. However, Sasaki (1985) noted that shrinkage was usually reported for larger male (>60 cm) and female (>70 cm) sablefish. This suggests that such occurrences are due to the combined influence of slow growth and measurement error. Furthermore, Beamish & Chilton (1982) noted that the freezing of commercially-caught fish could cause actual shrinkage. Interestingly, Beamish & Chilton (1982) also noted that data from freshly-caught fish measured by trained biologists occasionally showed shrinkage, indicating that shrinkage can occur in the ocean environment. Considering these factors, all recoveries, including those having negative growth increments, were used in the sablefish data analyses.

Although this species is extremely difficult to age (Kimura & Lyons 1991), age-determination criteria have been validated using oxytetracycline tags (Beamish & Chilton 1982) and radioisotope methods (Kastelle 1991). Because of the difficulty of directly determining ages for sablefish, estimating growth using tag-recapture data is of particular interest.

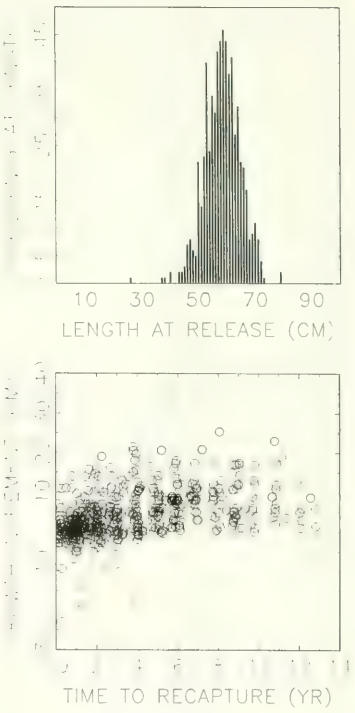

Figure 2

Length-frequency at time of release **(top)** and relationship between time at liberty and growth **(bottom)** for male sablefish in Gulf of Alaska.

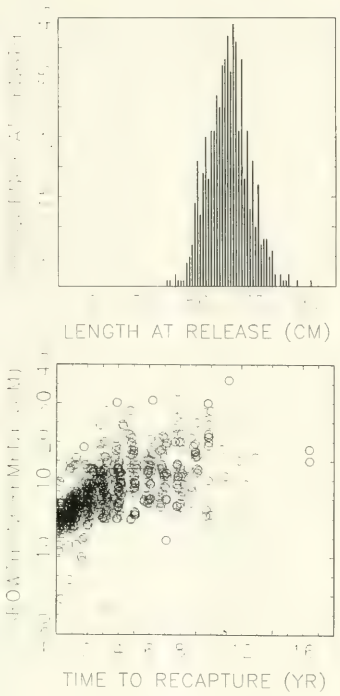

Figure 3
Length-frequency at time of release **(top)** and relationship between time at liberty and growth **(bottom)** for female sablefish in Gulf of Alaska.

Sablefish growth differs between regions, so we analyzed tag-recapture data from the Gulf of Alaska and the west coast of the United States separately (Fig. 1). Sablefish growth differs greatly by sex (Sasaki 1985), so it was necessary to estimate growth parameters for each sex.

Because the type of fishing gear used for tagging and recapture might affect the observed growth increments, we include tables of tagging and recapture gears for the usable data for all actual datasets (Table 2). Fish in the Gulf are primarily caught using longline gear, while fish off the west coast are primarily caught by trawl and pot gears.

For Gulf of Alaska sablefish, 133,558 fish were released, with 7946 recoveries between 1972 and 1990. Of these recoveries, 1340 had usable growth-increment information (Figs. 2,3). Longline gear dominated both tag and recovery gears (Table 2).

Table 2
Cross-tabulation of release and recovery fishing gears for Gulf of Alaska sablefish, west coast sablefish, and eastern Bering Sea Pacific cod. Only tag recoveries with usable growth-increment information are included. NA = not available.

		Recovery gear				
		NA	trawl	pot	longline	total
Gulf of Alaska sablefish						
Release	NA		1		2	3
gear	trawl		2	2	28	32
	pot	5	3	17	99	124
	longline	20	81	76	1004	1181
	total	25	87	95	1133	1340
West Coast sablefish						
Release	NA	1				1
gear	trawl	14	36	8	5	63
	pot	66	464	358	68	956
	longline	12	13	31	7	63
	total	93	513	397	80	1083
Eastern Bering Sea Pacific cod						
Release						
gear	trawl	19	175	4	86	284

Estimated von Bertalanffy parameters for sablefish in the Gulf of Alaska based on tag-recapture data can be compared with von Bertalanffy parameters estimated directly from length-at-age data (Table 3) from specimens collected on longline surveys in 1987 and 1989, and aged during 1990 and 1991 (Fig. 4). For this dataset the unweighted Fabens' estimates, the James' estimates, and estimates based on direct ages gave very similar parameter estimates. However, the weighted Fabens' estimates gave estimates quite different from the others.

Table 3
Comparison of von Bertalanffy growth parameters for sablefish in the Gulf of Alaska, estimated from tag-recapture and length-at-age data. Tag-recapture sample sizes: males n=643, females n=697. Direct-ages sample sizes: males n=807, females n=1165.

	L_∞	K_0	t_0	$SE(L_\infty)$	$SE(K_0)$	$SE(t_0)$
Males						
Unweighted Fabens	70.2	0.136		0.83	0.013	
Weighted Fabens	83.0	0.049		3.43	0.007	
James	70.7	0.126		2.84	0.044	
Length-at-age	70.2	0.120	–8.06	0.95	0.014	1.17
Females						
Unweighted Fabens	83.4	0.128		1.36	0.011	
Weighted Fabens	102.8	0.055		5.02	0.007	
James	84.7	0.117		3.53	0.024	
Length-at-age	86.7	0.106	–6.15	1.22	0.008	0.62

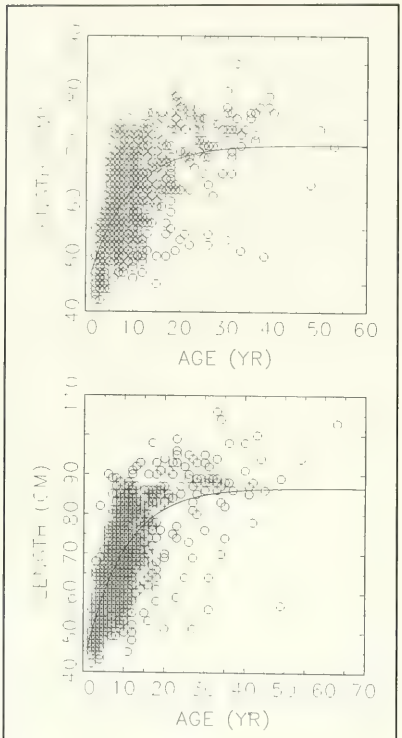

Figure 4
von Bertalanffy growth curves for male **(top)** and female **(bottom)** sablefish in Gulf of Alaska, calculated from length-at-age data.

For west coast sablefish, 52,743 fish were released, with 4220 recoveries between 1971 and 1991. Of these recoveries, 1083 had usable growth-increment information (Figs. 5,6). Pot gear was the dominant release gear, but both trawl and pot were important recovery gears (Table 2).

Estimated von Bertalanffy parameters for west coast sablefish based on tagging data can be compared with von Bertalanffy parameters estimated directly from length-at-age data (Table 4) from specimens collected in trawl and pot surveys in 1983 and 1989, and aged during 1991 and 1992 (Fig. 7). For this dataset, only James' estimates compared well with estimates based on direct ages. If James' estimates were not available, we could not conclude that estimates of growth parameters based on tagging were consistent with length-at-age data generated by age readers. Unexpectedly for the west coast dataset, James' estimates of $SE(L_0)$ were smaller than for the unweighted Fabens' estimates.

Another possible problem when analyzing growth-increment data is that the observed increments may be dependent on the tag or recovery gears that are used. Our west coast sablefish tag-recapture dataset provides an opportunity to examine whether observed growth increments may depend on the fishing gears used for tagging and recapture. From this dataset, we selected only fish with pot gear releases and trawl or pot gear recoveries. We then regressed growth increment against sex, recovery gear, size-at-release, and time at liberty. The analysis showed that fish recovered by pot gear could be expected to have growth increments 3.7 cm larger (significant α=0.0001) than fish recovered by trawl gear after the other independent variables were taken into account. Thus, release and recovery gears can be expected to affect the growth curves estimated from tag-recapture data.

Estimates from Pacific cod tag-recapture data

Pacific cod has also proved to be a very difficult species to directly age (Kimura & Lyons 1990). For eastern Bering Sea (Fig. 1) Pacific cod, 12,396 tagged fish were released, with 375 recoveries between 1982 and 1989. Of these recoveries, 284 had usable growth-increment information (Fig. 8). Bottom trawl was the only release gear, but both trawl and longline were important recovery gears (Table 2). Because of the small tag-recapture sample size available for Pacific cod, we combined male and female data into a single fit.

As with sablefish, Pacific cod tag recaptures can show negative growth increments (Fig. 8). For the complete tag-recapture dataset, unweighted and weighted Fabens' estimates were biased when compared with estimates based on length-at-age data (Table 5). James' estimates did not exist within a reasonable range for K_0 ($0.01<K_0<1.0$). Using recoveries with only positive growth increments allowed James' estimates to be close to those based on length-at-age data (Table 5). After deleting only the larger negative growth increments (i.e., larger in absolute value), data with increments greater than –10 cm gave a standard error for L_0 using James' method of 53.4 cm. These results indicate that for James' estimates, the sample size for Pacific cod was insufficient to overcome variability in the data.

Discussion

Our simulation study confirmed that James' robust estimators for estimating von Bertalanffy parameters from tag-recapture data show little bias when variability can be described by simple observational error and/or variability in L_∞. In contrast, the unweighted and weighted Fabens' estimators sometimes had

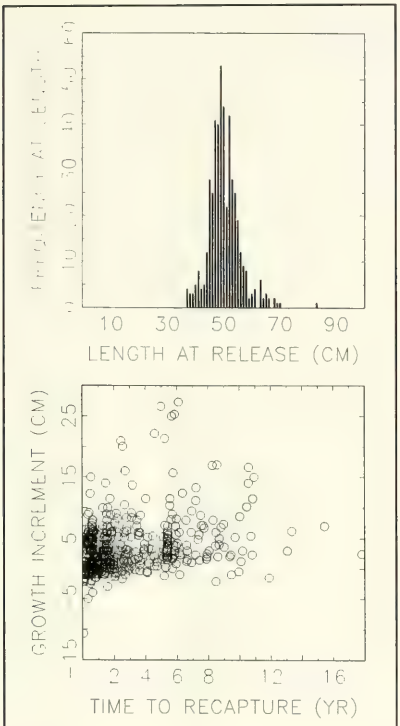

Figure 5
Length-frequency at time of release **(top)** and relationship between time at liberty and growth **(bottom)** for male sablefish off U.S. west coast.

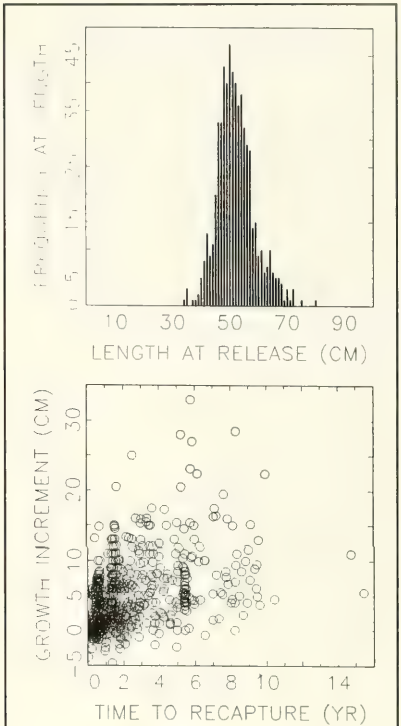

Figure 6
Length-frequency at time of release **(top)** and relationship between time at liberty and growth **(bottom)** for female sablefish off U.S. west coast.

Table 4
Comparison of von Bertalanffy growth parameters for sablefish off the U.S. west coast, estimated from tag-recapture and length-at-age data. Tag-recapture sample sizes: males n=467, females n=616. Direct-ages sample sizes: males n=714, females n=814.

	L_0	K_0	t_0	SE(L_0)	SE(K_0)	SE(t_0)
Males						
Unweighted Fabens	65.4	0.081		2.08	0.014	
Weighted Fabens	144.2	0.009		100.2	0.010	
James	56.6	0.556		0.65	0.108	
Length-at-age	54.7	0.472	−1.82	0.23	0.055	0.51
Females						
Unweighted Fabens	71.5	0.110		1.79	0.013	
Weighted Fabens	130.1	0.020		33.2	0.008	
James	61.4	0.481		0.92	0.085	
Length-at-age	61.0	0.499	−0.81	0.35	0.047	0.32

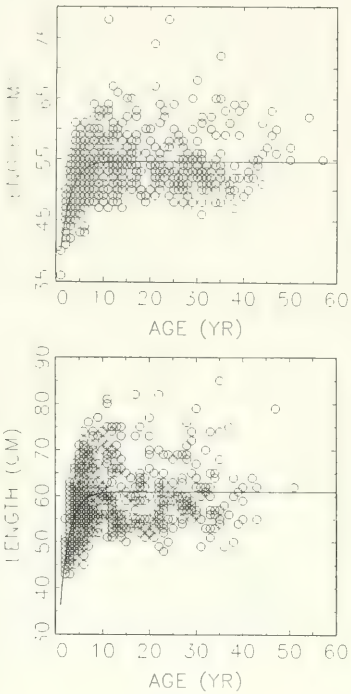

Figure 7
von Bertalanffy growth curves for male **(top)** and female **(bottom)** sablefish off U.S. west coast, calculated from length-at-age data.

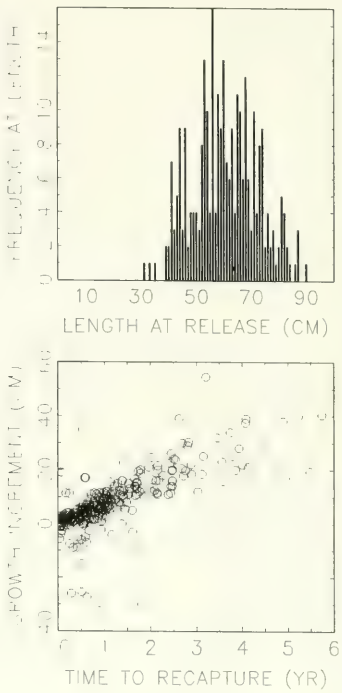

Figure 8
Length-frequency at time of release **(top)** and relationship between time at liberty and growth **(bottom)** for Pacific cod in eastern Bering Sea.

Table 5
Comparison of von Bertalanffy growth parameters for Pacific cod in eastern Bering Sea, estimated from tag-recapture data using all growth increments (n=284), only positive growth increments (n=252), and length-at-age data. Sexes were combined, and von Bertalanffy parameters estimated from length-at-age data were taken from Thompson & Bakkala (1990). NS = no solution, NA = not available.

	L_∞	K_0	t_0	SE(L_∞)	SE(K_0)	SE(t_0)
All growth increments						
Unweighted Fabens	117.0	0.148		9.69	0.029	
Weighted Fabens	271.0	0.035		147.81	0.024	
James	NS	NS		NS	NS	
Positive growth increments						
Unweighted Fabens	126.3	0.133		8.35	0.020	
Weighted Fabens	175.1	0.070		28.19	0.017	
James	104.3	0.222		10.55	0.065	
Length-at-age	105.4	0.237	1.06	NA	NA	NA

large biases. However, the standard errors for James' estimators tended to be larger, so in terms of mean square error the superior estimation method depended on the assumptions we made concerning variability.

Weighted Fabens' estimators performed well when error was restricted to observational error, but were badly biased when variability in L_∞ was introduced into the simulation. In contrast, James' estimators performed well when there was no observational error and error was due only to variability in L_∞. The unweighted Fabens' estimators were biased when error was solely observational, and biased when variability was due solely to variability in L_∞, but biases apparently canceled when both errors were present.

It is difficult to recommend the unweighted or weighted Fabens' estimators because they are both subject to large biases. It seems difficult to assume biases will cancel, or that there will be no variability in the data due to variability in L_∞.

On the other hand, the James' estimators appeared unbiased but tended to have larger standard errors. Our experience with analyzing the small sample-size dataset available for Pacific cod indicates that James' estimators may require at least moderate sample sizes, the required size depending on variability in the data. If sample sizes are sufficiently large, reducing bias can be far more important than increasing efficiency. Therefore, it seems important that James' estimators be used to at least guard against possible biases. More experience with James' method will probably be needed before researchers can finally decide the correct scope of application for this new method.

In this paper we have used von Bertalanffy parameter estimates based on direct ages as the yardstick by which to measure bias for the three different estimators. Of course, von Bertalanffy parameter estimates based on length-at-age data might themselves be biased. Except for the small sample-size dataset available for Pacific cod, James' estimators compared well with estimates based on direct age data. Unweighted Fabens' estimators compared well with estimates based on direct ages for one dataset. Weighted Fabens' estimators of L_0 appeared to be biased high for all three datasets.

This pattern of bias suggests that the tag-recapture data in these actual datasets contain significant amounts of variability due to variability in L_∞. This is also evidenced by the length-at-age data (see Figs. 4,7). For the three stocks of fish studied in this paper, we conclude that there are no inconsistencies in growth described by direct ages and growth described by tag-recapture data. Without James' estimators, this conclusion could not be made. We feel that James' method represents a significant step forward, and that datasets previously analyzed using Fabens' method might benefit by being reexamined using James' method. However, results may be the same as Fabens' estimates, or quite different, depending upon the nature of variability in the data.

Still, problems remain when evaluating growth from tag-recapture data. McFarlane & Beamish (1990) concluded that external tags could markedly affect the growth of sablefish. We have shown that different fishing gear types may select for slower- or faster-growing individuals. For the west coast sablefish tag-recapture datasets, growth increments appeared larger for fish recovered with pot gear compared with trawl gear. Therefore, sampling gears always play a role in describing the growth parameters we estimate.

Acknowledgments

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Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank*

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Abstract.–Vertical distribution patterns of haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* are summarized from eight research cruises on Georges Bank, during spring and summer 1981–86. Eggs and larvae were sampled at discrete depths with a 1 m^2 MOCNESS, pelagic juveniles with a 10 m^2 MOCNESS, and recently-settled juveniles with a bottom trawl supplemented with submersible observations. In well-mixed waters during early spring, eggs and larvae were distributed throughout the water column. Upon stratification of waters over the outer margin of Georges Bank in mid-May, the larval population was concentrated in the thermocline; the stronger the stratification, the more larvae were confined to this depth zone. At well-mixed shoal sites, pelagic larvae remained distributed throughout the water column.

Differences in day and night distribution patterns provided evidence to indicate that larvae began migrating as small as 6–8 mm; however, clear sampling differences were evident for larvae only at body lengths of >9–13 mm. Larvae tended to be deeper during the day and shoaler by night; larger larvae had a greater vertical range. Pelagic juveniles (>20 mm) occurred deeper in the water column as they grew. By mid-July most juveniles (~40 mm) were associated with the bottom. The transition from pelagic to demersal life (~40–100 mm) probably occurs over a period of 1–2 mo. Recently-settled juveniles remained demersal by day and migrated upwards 3–5 m at night. Their excursions off-bottom decreased in amplitude with larger sizes. Haddock remained closer to bottom both day and night at a smaller size than cod. The diel vertical behavior of cod may be strongly related to the light-dark cycle, whereas behavior of haddock was more variable. Some differences in vertical distributions between haddock and cod can be attributed to morphology and feeding behavior.

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On Georges Bank off the northeast coast of the United States (Fig. 1, page 293), stocks of haddock *Melanogrammus aeglefinus* L. and Atlantic cod *Gadus morhua* L. historically have been important components of the American and Canadian demersal fishery (Murawski et al. 1983, Overholtz & Tyler 1985). Eggs and larvae of both species are dominant in the spring ichthyoplankton community (O'Boyle et al. 1984, Sherman et al. 1984). Research survey data have shown that the size of a year-class is usually established by the end of the first year of life (Sissenwine 1984). At the Northeast Fisheries Science Center (NEFSC) since 1976, considerable research effort has been focused toward describing the place and time of spawning of haddock and cod, dispersal of eggs and larvae, and survival and recruitment of juveniles on Georges Bank. Field, laboratory, and modeling results were integrated to evaluate important mortality processes during the first year of life. Beginning in spring 1980, a series of interdisciplinary, process-oriented cruises used discrete depth samplers to investigate mortality due to starvation by describing the fine-scale spatio-temporal variability of gadid larvae in relation to their prey during the first few weeks post-hatching (Lough 1984, Laurence & Lough 1985). In 1984, a series of summer and early-fall surveys of juvenile gadids was initiated to document the distribution and abundance of the 0-group fish and their transition to the demersal phase when predation may be a dominant mortality factor (Cohen et al. 1988).

Based on these studies, we now have sufficient information to describe the life history of haddock and cod during the first 6–9 mo. Both species spawn on the northeast part of Georges Bank (Fig. 1). Peak spawning time for cod is late February–early March, and early April for haddock. The egg patches drift southwest a few kilometers per day in the clockwise residual drift and hatch within 2–3 wk (Lough 1984). By May, larval concentrations can be found along the southern edge of Georges Bank between the 60 m and 100 m isobath. In late-spring to fall, a seasonal thermocline develops to a depth of 10–30 m in waters deeper than ~60 m. Water shoaler than 60 m is vertically well-mixed throughout the year by the strong (>60 cm/s) rotary tidal currents. Larvae >30 d can be found shoaler than the 60 m isobath as the patch moves southwest, and by late June some fraction of the population has moved onto the shoals of western Georges Bank (Walford 1938,

*MARMAP Contribution FED/NEFC 90-01, Woods Hole Laboratory, Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA.

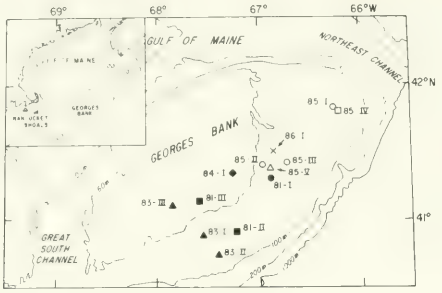

Figure 1

Location of vertical distribution studies, 1981–86, on Georges Bank, designated by year and sampled sites. Sites (Roman numerals) within a cruise have same symbols.

Lough 1984, Smith & Morse 1985, Lough & Bolz 1989). By late July–early August, the highest catches of juvenile gadids are usually found on eastern Georges Bank (Lough et al. 1989).

Haddock and cod undergo typical development and morphological transformation at sizes >20 mm standard length (SL, ~2–3 mo post-hatching) (Fahay 1983, Auditore et al. 1993). Their transition from pelagic to demersal life occurs when they are >25 mm in midsummer (Lough et al. 1989).

Information on larval and juvenile vertical distributions and diel migrations are needed to (a) study their transport by currents, (b) compare vertical distributions of their prey and predators, and (c) make accurate abundance estimates of various stages caught by different sampling gear. In this paper we summarize data on the vertical distribution of 0-group haddock and cod during spring and summer on Georges Bank from 1981 to 1987. The following questions on the early life of haddock and cod were addressed. (1) What is the vertical distribution pattern of larvae and juveniles on Georges Bank? (2) What is the timing and range of diel migratory behavior in relation to development? (3) What is the transition period from pelagic to demersal life for an individual fish? (4) How do light, temperature, salinity, and currents influence vertical distribution and migratory behavior? (5) How does gear selectivity bias vertical distribution patterns?

Methods

Sampling protocol

General cruise objectives and sampling strategy for the larval–juvenile fish studies are described by Lough (1984). A concentration of larvae on Georges Bank was located by a fine-scale grid of stations using standard bongo-net gear. Based upon real-time sample analyses made during the grid survey, sites were selected within well-mixed and stratified waters for the comparative vertical time-series observations. Haddock and cod were collected by three gear types on eight cruises (Table 1). Pelagic larvae and juveniles were sampled with an electronically-controlled, multiple opening/closing net and environmental sensing system (MOCNESS), with a 1 m^2 or 10 m^2 mouth opening (see Wiebe et al. 1976, 1982, 1985). A Yankee 36 bottom trawl was used to sample the recently-settled juvenile fish. The numbers of day, night, and twilight hauls at each site are listed in Table 1.

The MOCNESS used to sample the larval stage has an effective mouth opening of 1 m^2 when towed at a 45° net angle near 3.7 km/h (2 kn). The unit consists of nine 0.333 mm mesh nets that open and close sequentially on command. Temperature (and salinity beginning in 1985) was obtained simultaneously with standard net-sampling parameters such as depth and volume of water filtered. When a concentration of larvae was located, a drogue was deployed at a depth of 15 m to mark the water mass for further sampling. Thereafter, the 1 m^2 MOCNESS was used to sample every 3–6 h at the drogue for a period of 24–48 h. Discrete depths were sampled at 10 m intervals from the surface to within 5 m of the bottom within a 5 min period. Each net filtered ~250 m^3 of water.

The 10 m^2 MOCNESS, used to collect the pelagic juveniles, has five 3.0 mm mesh nets. Because juveniles tend to remain localized for at least 2–4 d, sampling was conducted at fixed sites that were determined to contain high concentrations of juveniles. The vertical distribution of pelagic juveniles was sampled every 6 h. Discrete depth strata ranged 10–30 m from the surface to within 5 m of the bottom; each net filtered between 15,000 and 20,000 m^3 of water during a 30 min tow.

A Yankee 36 bottom trawl was used to catch recently-settled juveniles. Trawl specifications are found in Azarovitz (1981). The opening height and width of the trawl was 3.2×10.4 m. The trawl had graded stretch mesh of 127–13 mm (mouth to cod-end). Standard roller gear (40.6 cm diameter) was used on the *Albatross IV* 86-03 June 1986 cruise; however, rollers were replaced with a sweep chain of rubber disks (11.4 cm diameter) on the *Delaware II* cruises 85-05 of July 1985 and 85-06 of August 1985, to collect fish close to bottom. The standard bottom-trawl set was made at 6.5 km/h (3.5 kn) for 30 min on the bottom. Trawl sampling was conducted for 24 h.

All specimens were initially fixed in either 4% formaldehyde-seawater solution or 90% ethyl alcohol and

then subsequently preserved in 70% ethyl alcohol and water. Temperature and salinity profiles were obtained from the MOCNESS, XBT drop, or CTD cast.

Data analysis

Larvae and pelagic juveniles were measured to the nearest 0.1 mmSL. Demersal juveniles from the bottom trawl were measured to the nearest mm. Length of haddock and cod were corrected for shrinkage to live-length using the method of Bolz & Lough (1983). Catches from the 1 m^2 MOCNESS were initially standardized to $n/100\ m^3$ of water, and 10 m^2 MOCNESS catches to $n/10{,}000\ m^3$. The fish were grouped into size-classes based on developmental characters (Auditore et al. 1993): 2–5, 6–8, 9–13, 14–19, 20–29, 30–39, 40–49, 50–59, and 60–69 mm.

As an initial step, the percent of a size-class at each depth was plotted with the temperature and salinity profile for each tow (figures not shown). Tows were classified as day, night, or (in a few cases) twilight, i.e., 1 h before and after sunrise and sunset. For each pelagic tow, the mean number of fish within a time-block and size-class was calculated for each depth by summing all hauls at that site. Day and night vertical profiles are plotted from these arithmetic means. Also, abundance of larvae was integrated over the water column, in terms of $n/10\ m^2$ for the 1 m^2 MOCNESS catches and $n/1000\ m^2$ for the 10 m^2 MOCNESS catches. Abundance-weighted mean depth or center of density distributions of size-classes were calculated using the method of Miller et al. (1963). To examine trends, mean depths of selected sites were plotted in time-series with water column thermoclines. Since salinity changes throughout the water column are generally small (<1 psu), temperature usually has a dominant effect on density and stratification of the surface water on Georges Bank (Flagg 1987).

To test for differences in population means between day and night vertical distributions and for interactions among depth, time of day, and size of fish, an unbalanced ANOVA Type-III model was used on all tow data (Dunn & Clark 1974). The linear model is:

$$Y = b_0 + b_1(D) + b_2(T) + b_3(S) + b_4(D\times T) + b_5(D\times S) + b_6(T\times S) + b_7(D\times T\times S) + e, \quad (1)$$

where Y is fish density (n/m^3), D is depth effect (coded depth level), T is time effect (coded night or day), S is size effect (coded size-class), b is a constant, and e is the normally-distributed residual error term. Transformation of the fish density data by $\log_{10}(x+0.1)$ resulted in a normal distribution of the residuals. Although the interpretation of vertical migration based on ANOVA can be difficult, the depth × time interaction is generally considered the most useful factor for detecting diel migrations (Sokal & Rohlf 1969). Summary tables are presented of the factor F-values and their level of significance.

For each station, an average temperature and salinity profile was made by summing all the time-series data across the sampled depth levels and calculating the mean, standard deviation, and 95% confidence limits. At sites where stratification of the water column occurred primarily from solar insolation, upper and lower bounds of the thermocline region were determined by inspection for each tow profile. The thermocline was defined as the region of greatest temperature change. In a well-stratified water column, the zone of greatest temperature change was easily identified between the relatively uniform water above and below this zone. In a weakly-stratified water column, determination of the thermocline zone was more subjective. The distribution of larvae within, above, and below the thermocline was estimated for each size-class within a tow at Sites I&II for May 1983. The mean percentage distribution and standard error of each region were calculated on the angular transformation of the tow percentage data: angle = arcsin $\sqrt{\text{proportion}}$.

Bottom-trawl catches of recently-settled juvenile haddock and cod were standardized to $n/30$ min haul. Length data were grouped by 1cm size-classes and then grouped by day, night, and twilight catches. Standard statistics ($\bar{x}$, SD, CV) were calculated on the untransformed data. Differences between population means were tested by the Students' t-test on $\log_{10}$ transformed data (Sokal & Rohlf 1969).

Results

Vertical distribution of larvae

Well-mixed water In April 1981, recently-hatched haddock larvae (2–5 mm) and fewer larger larvae (6–8 mm) were distributed throughout the water column (Fig. 2A). Results of the ANOVA for the 2–5 mm haddock (Table 2) showed a significant effect of depth ($p<0.05$) but not of time of day.

Cod larvae (up to 8 mm) also were distributed through the water column (Fig. 2B). In several vertical profiles the distributions are weakly bimodal. During the day, larger larvae (9–29 mm) were most abundant at mid-depth, 30–40 m, whereas at night they were more abundant above 30 m. Ratios in night-day abundance increased from ~2/10 m^2 or less for the smaller larvae (<14 mm) to 4–6/10 m^2 for the 14–19 mm and 20–29 mm size-classes. ANOVA for cod larvae showed a significant ($p<0.05$) interaction effect of time × size, which was expected since abundance increases at night as cod get larger (Table 2A). A significant ($p<0.05$) depth × time interaction occurred only for size-classes >9–13 mm.

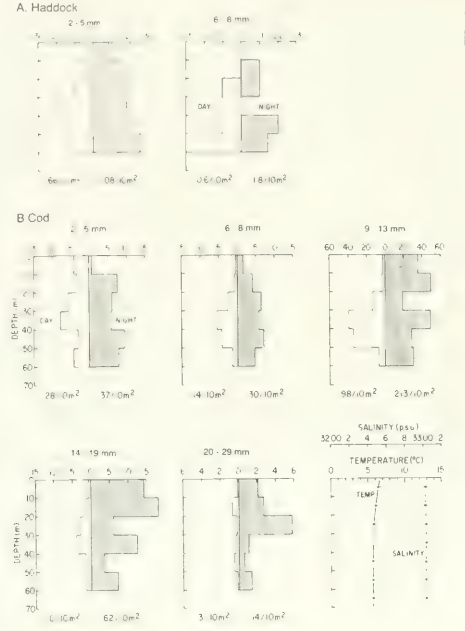

Figure 2

Mean day and night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by the 1 m^2 MOCNESS on well-mixed Site 81-I during 27–29 April 1981. Estimated water column abundances (n/10 m^2) are included for day-night comparisons at bottom of plots. Composite temperature and salinity profiles are plotted as depth stratum mean (●) and 95% confidence limits (— —).

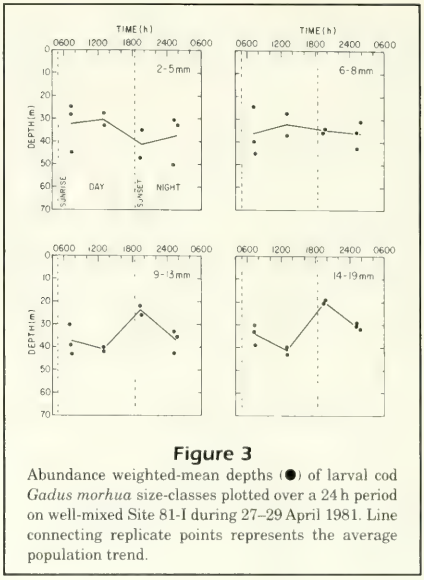

Figure 3

Abundance weighted-mean depths (●) of larval cod *Gadus morhua* size-classes plotted over a 24 h period on well-mixed Site 81-I during 27–29 April 1981. Line connecting replicate points represents the average population trend.

Mean depths of the four smallest cod size-classes are plotted for each tow within a 24 h period over the 2.5 d of sampling at Site 81-I, and a trend line connects the mean depths of abundance (Fig. 3). There appears to be a daily pattern in vertical distribution. The smaller size-classes, 2–5 mm and 6–8 mm, remained at a depth of ~35 m day and night. In contrast, larger size-classes of cod, 9–13 mm and 14–19 mm, showed a consistent diel migration from a mean depth of 40 m at noon to 20–25 m after sunset.

At the well-mixed shoal (35–58 m) Site 81-III on 27 May 1981, 2–13 mm haddock and 6–13 mm cod larvae were distributed through the water column (Fig. 4) with mean depths of abundance generally at 20 m and 40 m. Because of the limited number of tows, a significant difference in day-night patterns could not be determined.

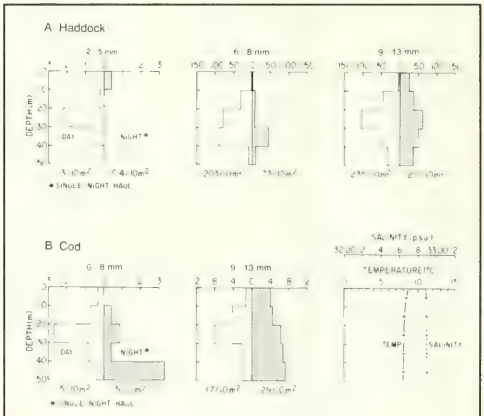

Figure 4

Mean day and night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by the 1 m^2 MOCNESS on well-mixed Site 81-III during 27 May 1981. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

At the well-mixed shoal (34–54 m) Site 83-III on 16–17 May 1983, three size-classes of haddock and cod larvae (6–8, 9–13, 14–19 mm) were distributed through

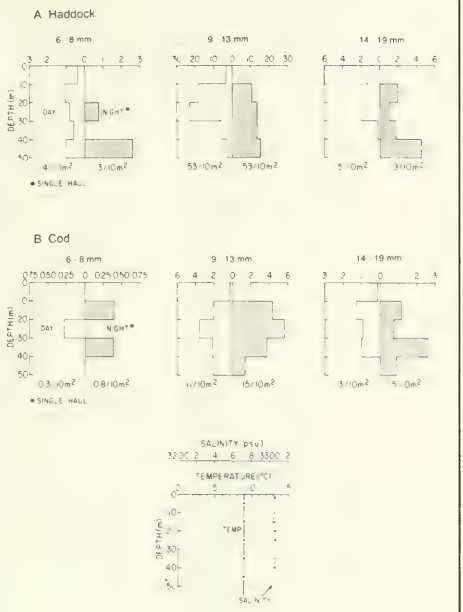

Figure 5

Mean day and night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by the 1 m^2 MOCNESS on well-mixed Site 83-III during 16–17 May 1983. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

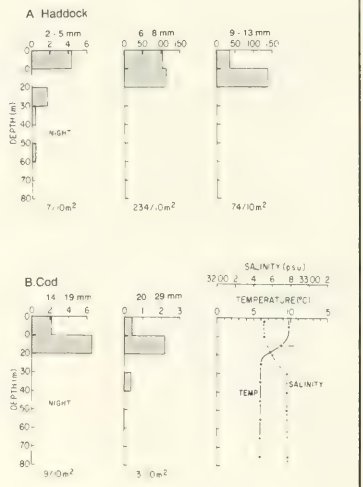

Figure 6

Night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by a single 1 m^2 MOCNESS tow on well-stratified Site 81-II before the storm on 21 May 1981. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum mean (●) and 95% confidence limits (— —).

the water column (Fig. 5). The single night haul and low densities preclude firm conclusions.

Stratified water On 21 May 1981, when the water column at Site 81-II (75–83 m) was strongly stratified, a single 1 m^2 MOCNESS night tow found haddock and cod larvae 2–13 mm to be confined almost exclusively to the upper 20 m of the water column, and maximum densities usually were within the strong thermocline gradient at 10–20 m depth (Fig. 6). No recently-hatched cod larvae 2–5 mm were caught in this tow. The surface temperature approached 10°C with a strong thermal gradient at 11–21 m, where the temperature decreased to 5.9°C. An intense storm on 21–24 May 1981, with winds up to 18–21 m/s (35–40 kn) and sea wave heights of 3–5 m (10–15 ft), destroyed the strong thermocline shown in Fig. 6. Following the storm, the water column was well mixed and the larvae were distributed broadly (Fig. 7), but about an order of magnitude more abundant relative to the collections made on 21 May. Differences in mean day and night vertical distributions of larvae during the well-mixed period of 24–26 May 1981 indicate a diel shift in distribution patterns of the larger larvae (Fig. 7), with population centers located deeper in the water column by day (40–60 m) and shoaler by night (10–40 m). This diel shift in vertical distribution is supported by the ANOVA (Table 2B), where both haddock and cod have significant (p<0.05) depth × time interaction effects. By 28 May 1981, near-surface insolation warming of the upper 20 m occurred, and larvae reaggregated above 20 m near a weak thermocline (Fig. 8).

Mean depths of larvae captured in tows before and after the storm are plotted in Fig. 9 along with depth bounds of the thermocline region. The weak thermocline deepened after 25 May 1981. Mean depths of larval abundance remained below the weak thermocline until 28 May. Tows made on 26 May showed that the larger larvae were mainly located deeper in the

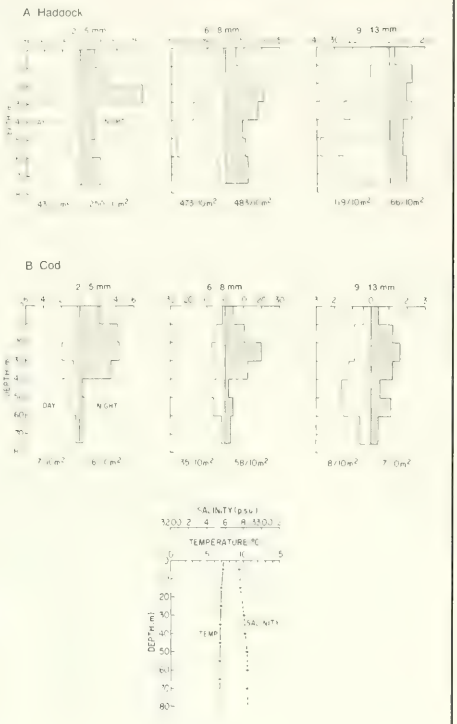

Figure 7

Mean day and night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by the 1 m^2 MOCNESS on well-mixed Site 81-II following the storm on 24–26 May 1981. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

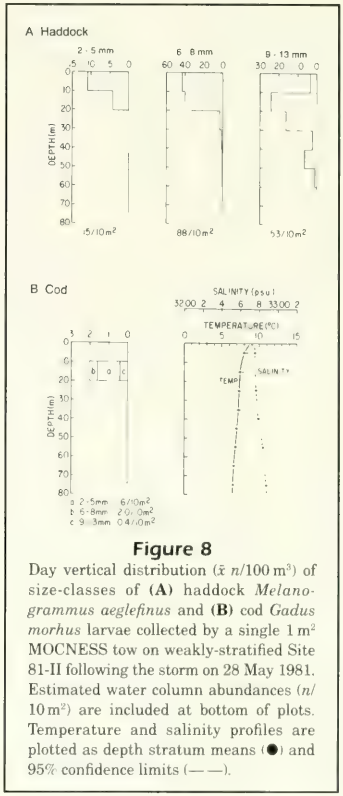

Figure 8

Day vertical distribution ($\bar{x}$ n/100 m^3) of size-classes of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhus* larvae collected by a single 1 m^2 MOCNESS tow on weakly-stratified Site 81-II following the storm on 28 May 1981. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

water column than smaller larvae. However, when the water column was well-stratified on 21 May and weakly-stratified on 28 May, in both day and night all sizes of larvae were located in or above the thermocline. The single day and night tows were not sufficient to base firm conclusions on diel differences.

In mid-May 1983, two sites were sampled in weakly-stratified waters across the southern margin of Georges Bank. At Site 83-I (Fig. 10), mean day and night vertical distributions show haddock and cod larvae distributed broadly through the water column on 13–14 May, but each of the three size-classes had a different depth distribution. Recently-hatched larvae (2–5 mm) were most abundant at 10–30 m both day and night. The 6–8 mm size-classes of both species were more broadly distributed and most abundant at 10–50 m depths, with haddock tending to be deeper in the water column by day than cod. The 9–13 mm size-class for both haddock and cod had a pronounced diel shift in day-night distribution patterns: most larvae were in the lower half of the water column by day but in the upper half at night. The maximum density for both species was at 10–20 m. There were significant (p<0.05) interactions for each combination of depth, time, and size (ANOVA; Table 2C).

A time-series of larval catches in relation to the thermocline region at Site 83-I is shown in Fig. 11. Although the mean depth of the thermocline centered at ~20 m, its bounds varied between 10 and 40 m, perhaps due to the tides. While the population centers of cod and haddock larvae tended to be associated with

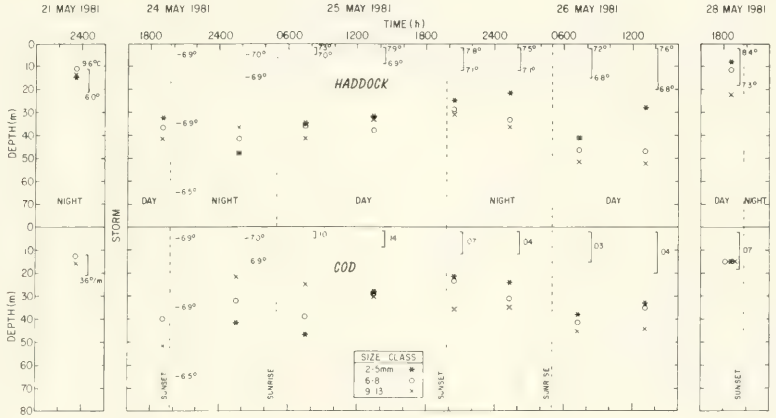

Figure 9

Time-series of abundance weighted-mean depths of larval haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* size-classes on Site 81-II before and after the storm on 21–28 May 1981. Brackets at tow time record upper and lower depth bounds of the thermocline region. In the haddock time-series, boundary temperatures are recorded beside the brackets; for cod, the rate of temperature change ($\delta T/\delta Z$) over the thermocline region is specified. Where no thermocline was evident, temperatures at selected depths are inserted.

the thermocline region, they were not confined exclusively to it, as in May 1981 when the water column was strongly stratified. Larger larvae of both species tended to be found at greater depths during the day, especially the 9–13 mm larvae.

At Site 83-I, >64% of the 9–13 mm size-class for both haddock and cod was found below the thermocline by day, but <28% by night (Table 3A). A significantly ($p<0.05$) greater percentage of the 9–13 mm size-class was found within and above the thermocline at night. For the 2–5 mm size-classes, haddock and cod larvae were found mostly within or above the thermocline; <15% were located below the thermocline, and there was no significant day-night difference in the profile percentages. For the 6–8 mm size-classes of haddock and cod, the highest percentage of larvae were located within the thermocline. Of the haddock larvae, 40% were found below the thermocline by day, but only 18% at night ($p<0.005$). There was no significant change in the day-night percentages for 6–8 mm cod.

On 15–16 May 1983, at Site 83-II (88–93 m) near the shelf/slopewater front, thermocline depth was somewhat deeper with a smaller gradient than at Site 83-I. Most haddock and cod larvae were confined to the upper 40 m, the lower bound of the thermocline (Fig. 12). A small percentage of larger larvae (9–13 mm) were located below the thermocline by day (13% for haddock and 20% for cod) but moved nearer the surface by night (Table 3B). All size-classes of larvae were broadly distributed within the upper part of the water column. There were significant (ANOVA; $p<0.001$) effects of depth, time, and size for haddock; only depth × size interaction was significant ($p<0.01$) for cod (Table 2C). Mean depths of haddock and cod were greater by day for the larger larvae, especially for the 9–13 mm size-classes (Fig. 13), and in all but one night tow the mean depths were located within the confines of the thermocline region.

Vertical distribution of pelagic juveniles

In June 1984, pelagic juvenile haddock and cod were collected at a well-mixed shoal (40–49 m) Site 84-I (Fig. 14). Cod were more abundant than haddock at Site 83-I, and the larger fish (14–29 mm) were caught more abundantly in night tows than day. The three size-classes of haddock were similarly distributed throughout the water column. Few were caught in the upper 10 m; abundance usually peaked near 10–20 m both day and night. Pelagic cod also were caught throughout the water column during the day, with abundance peaks near 10–20 m for the 14–19 mm and 20–29 mm size-classes. They were more abundant in

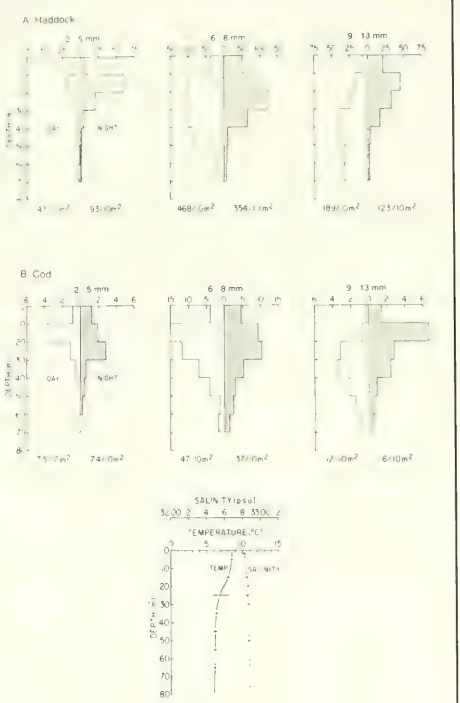

Figure 10

Mean day and night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by the 1 m^2 MOCNESS on weakly-stratified Site 83-I during 13–14 May 1983. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

the upper half of the water column at night, increasing somewhat towards the surface. There were no significant interaction effects in the ANOVA for either cod or haddock (Table 4).

On 18–22 June 1986 at a well-mixed deeper (65–78 m) Site 86-I, cod juveniles 14–49 mm were caught (Fig. 15). Mean day and night vertical distributions show a clear pattern of larger size-classes of cod located progressively deeper in the water column, with the 40–49 mm cod located almost entirely between 50 m and the bottom. Night catches were greater than day catches for all size-classes of cod. Night mean abundance was significantly greater (ANOVA; $p<0.01$) than day mean abundance of the 20–29 mm and 30–39 mm size-classes (Table 4). There was no detectable evidence of diel vertical migrations.

By July, relatively few pelagic haddock and cod juveniles were caught. Highest densities of juvenile gadids were located on eastern Georges Bank (Lough et al. 1989). Three sites were sampled in mid-July 1985 on eastern Georges Bank: Site 85-I (82–87 m), stratified; Site 85-II (64–72 m), weakly stratified; Site 85-III (78–83m), stratified (Fig. 16). The deeper Sites 85-I & 85-III both had a gradual thermocline at 15–30 m depths. Only a few pelagic cod juveniles were caught. Pelagic cod ranging 30–59 mm were caught mostly at night, although a day tow was not made at Site III. Relatively few fish were caught in the upper 30 m, and there was a tendency for the highest densities to be located in the bottom third of the water column. Cod were caught in day tows at Site 85-I in the bottom 60–80 m stratum.

Diel migration of recently-settled juveniles

In 17 bottom trawls (with rollers) at Site 86-I, 25–26 June 1986, demersal cod juveniles with a mean length of 4–5 cm were collected (Table 5). Few were caught in day trawls, but at least an order of magnitude more cod ($\bar{x}$ 103/30 min trawl) were caught in night trawls. During 17–18 July 1985 at Site 85-IV, nine bottom trawls (with rubber disk sweep chain) were made (Table 6; Fig. 17). Both haddock and cod appeared to be caught more abundantly in day trawls than at twilight. Only one haddock juvenile was caught in the single night trawl. The mean length of haddock was 7.1 cm (range 4–10 cm), and 5.5 cm for cod (range 2–12 cm). Mean lengths of both species were the same in day and twilight trawls. The high daylight catches of cod juveniles in this series are in contrast to the high night catches of cod of the same average size, 4–5 cm, in June 1986 using a bottom trawl with rollers. Gear difference (rubber disks vs. rollers) may have been the cause of the different day-night catches, but conclusions cannot be made because in July 1985 only one night trawl was made.

During 16–17 August 1985, 12 bottom trawls (with rubber disk sweep chain) on southeastern Georges Bank (63–71 m), Site 85-V, caught relatively high numbers (210–257/30 min trawl) of 9–19 cm haddock juveniles (Table 7; Fig. 18). The mean number and lengths of fish per trawl were not significantly different ($p>0.05$) by paired t-tests for the night, day, and twilight catches.

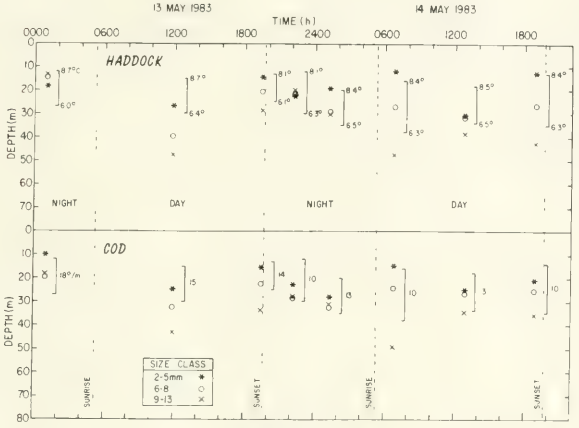

Figure 11

Time-series of weighted-mean depths of **(A)** larval haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes on weakly-stratified Site 83-I during the period 13–14 May 1983. In the haddock time-series, boundary temperatures are recorded beside the brackets; for cod, the rate of temperature change ($\delta T/\delta Z$) over the thermocline region is specified.

Sampler retention and avoidance

The 1 m² MOCNESS sampled effectively on a horizontal scale of 0.2–0.3 km; the 10 m² MOCNESS, 1–2 km; and the bottom trawl, 3–4 km. Minimum length of fish fully retained and not extruded by the various nets was estimated using a model based on the stretch mesh size and a body height-to-length regression (Potter et al. 1990). These estimates indicated that almost all haddock and cod larvae >~4 mmSL are retained by the 1 m² MOCNESS 0.333 mm mesh nets. For the 10 m² MOCNESS, 3.0 mm mesh nets, haddock <17 mm and cod <15–16 mm probably are not fully retained. Minimum size retention of juvenile fish collected by the research bottom trawl is 31–37 mm.

The 1 m² MOCNESS night-day abundance ratios (n/10 m²) are shown in Table 8, page 307 for size-classes of cod and haddock collected in April and May 1981 and May 1983. The total night-day ratios for cod are ~1.2 for the 2–5 mm and 6–8 mm size-classes, near 2.0 for the 9–13 mm size-class, and to ~4.0–6.0 for the 14–19 mm and 20–29 mm size-classes (Fig. 19). An exponential curve fit appears to adequately describe the increase of night-to-day catch ratios with increasing size of fish. Cod appear to visually avoid the 1 m² MOCNESS net by day at all lengths, especially after reaching 9–13 mm. Day abundances of haddock are greater than night for the 6–8 mm and 9–13 mm size-classes, which may indicate a different avoidance behavior at this size.

The 10 m² MOCNESS night-day abundance ratios (n/1000 m²) are shown in Table 9 for size-classes of cod and haddock from study sites in June 1984, 1986, and July 1985. A greater size-range of cod is available than for haddock. For cod, the smallest (9–3 mm) and the largest (50–59 mm) size-classes are not fully vulnerable to the net, due to extrusion of the smallest larvae through the net mesh and distribution of the largest juveniles below the sampling depth. The total night-day ratios for cod are ~2–3 (range 1.49–3.05) for size-classes 14–19 mm through 40–49 mm. Haddock juveniles have night-day ratios of ~3–4 for the 14–19 mm and 20–29 mm size-classes.

Discussion

The difficulty of detecting vertical migration in planktonic organisms, given the high sampling variability and limited resources for replicate time-series of observations as well as gear limitations, has been discussed by Pearre (1979), Shulenberger (1978), Denman & Platt (1978), and others. We are forced to look for repeatable patterns, often in the absence of statistical proof. Because of these difficulties, diverse observations have been reported in the literature. In this study, the vertical distribution patterns and diel migrations of haddock and cod larvae and juveniles have been documented in stratified and well-mixed waters of Georges Bank in greater detail than previously seen because of electronic MOCNESS samplers and the use of submersibles.

Sampler avoidance

Many investigators have reported night-day catch ratios >1. Net avoidance usually is greater for day than night tows because of visual detection of the net (Morse 1989). In another Georges Bank study using the 10 m² MOCNESS, Potter et al. (1990) reported night catches of pelagic cod juveniles averaging 30 mm to be signifi-

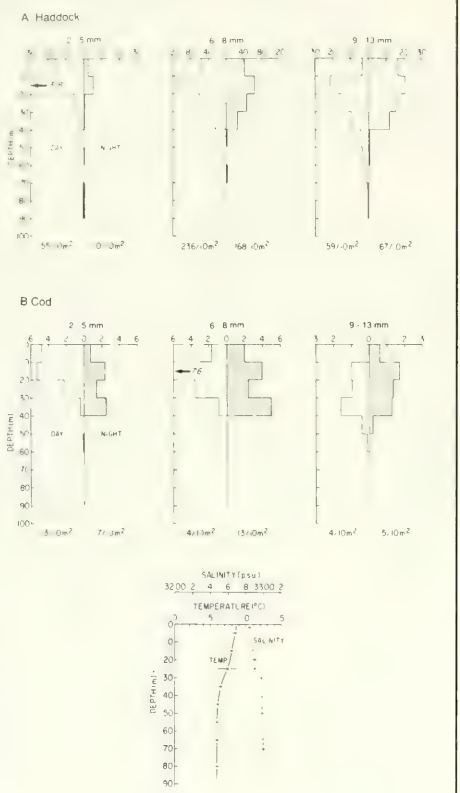

Figure 12

Mean day and night vertical distribution ($\bar{x}$ n/100 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of larvae collected by the 1 m^2 MOCNESS on weakly-stratified Site 83-II during 15–16 May 1983. Estimated water column abundances (n/10 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (—).

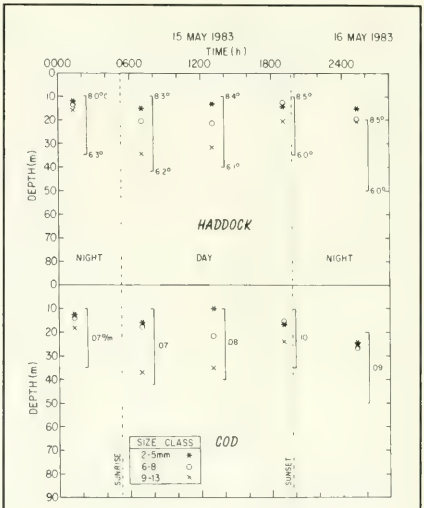

Figure 13

Time-series of abundance weighted-mean depths of larval haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* size-classes on weakly-stratified Site 83-II during the period 15–16 May 1983. In the haddock time-series, boundary temperatures are recorded beside the brackets; for cod, the rate of temperature change (dt/dz) over the thermocline region is specified.

cantly greater than day catches. Their average night-day catch ratio for 16–45 mm cod was 3.0 (range 1.6–4.7), which is similar to the ratios estimated in this study of cod and haddock pelagic juveniles.

In an extensive study of the northeast U.S. continental shelf ichthyoplankton (an 8 yr time-series of data using a 61 cm diameter bongo net, standard MARMAP double-oblique tows), Morse (1989) found larval haddock to be the exception among most taxa in that day catches exceeded night catches for all lengths of larvae in the range 4–15 mm. Day catches were somewhat greater than night catches for 4–12 mm cod, but for the larger fish (13–20 mm) night catches were equal to or greater than day catches.

Haddock larvae, as well as cod, may remain still during the day to evade predator detection by visual or mechano-reception (Zaret 1980). When both haddock and cod reach a larger size and their sensory systems become more developed, they exhibit a startle response and evade the attacking predator (in this case a net) (Blaxter & Fuiman 1990). Flexion and fin ray development is complete for both species at 15–20 mm (Auditore et al. 1993) and they would be more capable of a powerful darting speed. Perhaps at night without visual stimuli, only the larger juveniles exhibit a startle response to the net-mouth pressure stimulus. Light-aided avoidance is expected to decrease with water depth as a function of light attenuation and the fishes' visual threshold (Blaxter & Fuiman 1990). Pressure

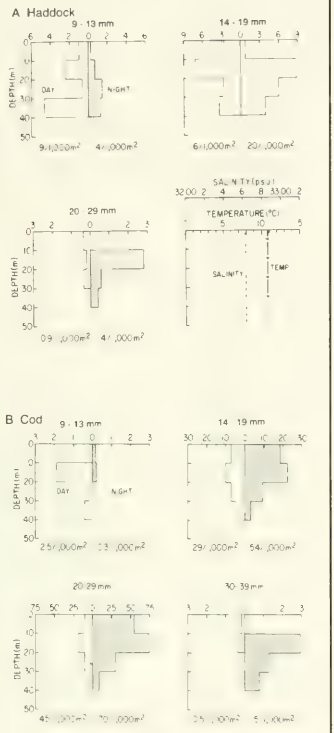

Figure 14

Mean day and night vertical distribution ($\bar{x}$ n/10,000 m^3) of **(A)** haddock *Melanogrammus aeglefinus* and **(B)** cod *Gadus morhua* size-classes of pelagic juveniles collected by the 10 m^2 MOCNESS on well-mixed Site 84-I during 17–19 June 1984. Estimated water column abundances (n/1000 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

or sound avoidance are expected to be the same over depth, however.

Therefore, for the three smallest size-classes of haddock and cod <13 mm, light-aided avoidance of the 1 m^2 MOCNESS sampler may be relatively small (< factor of 2) as a contributing factor in observed day-night vertical distribution patterns. However, in fish >14 mm, night-day catch ratios are expected to increase to >3 because of light-aided avoidance response. Haddock larvae appear to respond differently to light than cod in their avoidance behavior. A correction factor for cod was not applied from the water-column total abundance ratios. The night-day catch ratios are not suitable for correcting depth strata densities, since net avoidance may be a function of light level which decreases with depth. That is, avoidance may be depth-dependent. We do not have the data suitable for making an appropriate depth correction. Applying a constant correction factor to all depth levels of a given size-class would not change the vertical distribution pattern. We need to know the fishes' reaction distance to the net at the different depth light levels.

During the fishes' transition from a pelagic to demersal life at ~30–40 mm, they are not fully vulnerable to either pelagic or demersal sampling gear and this contributes to the sampling variability. Scott (1984) studied diel variations in juvenile haddock catch rates from a 24 h bottom-trawl experiment near Sable Island on the Scotian Shelf in July–August. Haddock >6 cm had a marked vertical migration pattern, moving off the bottom at night and returning by daylight. Based on changes in mean lengths, larger fish moved off the bottom in greater proportions than smaller fish. Colton (1965) examined data from bottom-trawl surveys conducted on Georges Bank and found catch-per-tow of 0-group and 1+ yr haddock to be markedly higher during the night than day. He believed the night-day variability was due to escapement from the net during the day and not to avoidance. Lough et al. (1989) conducted submersible studies on eastern Georges Bank in July 1987 and August 1986 and found recently-settled juvenile gadids (mostly cod) 4–12 cm in length close to the bottom (<0.5 m) during the day and a portion of the population rising 1–5 m off the bottom at sunset, drifting with the current. A comparison of standardized research bottom-trawl (with rollers) catches and submersible transect counts showed the extent of undersampling by the bottom trawl. For 4 cm modal-size cod (1987), daylight trawl abundance estimates were at least an order of magnitude lower than the submersible transects, but not significantly different than the night estimates. For demersally-oriented larger fish (7 cm modal length), few fish were caught by daylight trawls, and night trawl catches were still at least an order of magnitude lower than night submersible counts. The larger fish appeared to stay closer to the bottom both day and night, and consequently they are less vulnerable to the bottom trawl with roller gear which may pass over them. Some preliminary results by Cohen et al. (1985) showed that more cod juveniles of 4–5 cm were caught using the bottom trawl with the smaller rubber disc-covered chain sweep than with the larger roller gear. Thus, the bottom trawl catches of recently-settled cod are known to have a significant sampling bias with more cod collected in night trawls than day, and especially for the larger fish escaping the roller gear.

Vertical distribution patterns

The initial depth distribution of recently-hatched larvae is dependent upon the late-stage egg distribution. Some limited egg profile data

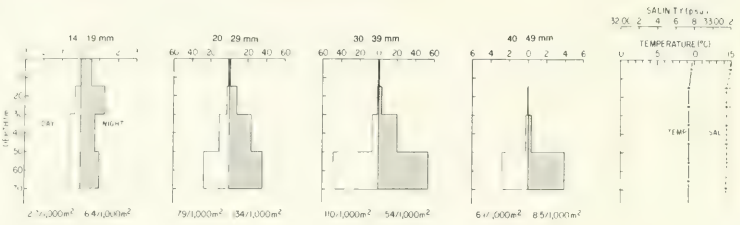

Figure 15

Mean day and night vertical distribution ($\bar{x}$ n/10,000 m^3) of cod *Gadus morhua* size-classes of pelagic juveniles collected by the 10 m^2 MOCNESS on well-mixed Site 86-I during 18–22 June 1986. Water column abundances (n/1000 m^2) are included at bottom of figure. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits (— —).

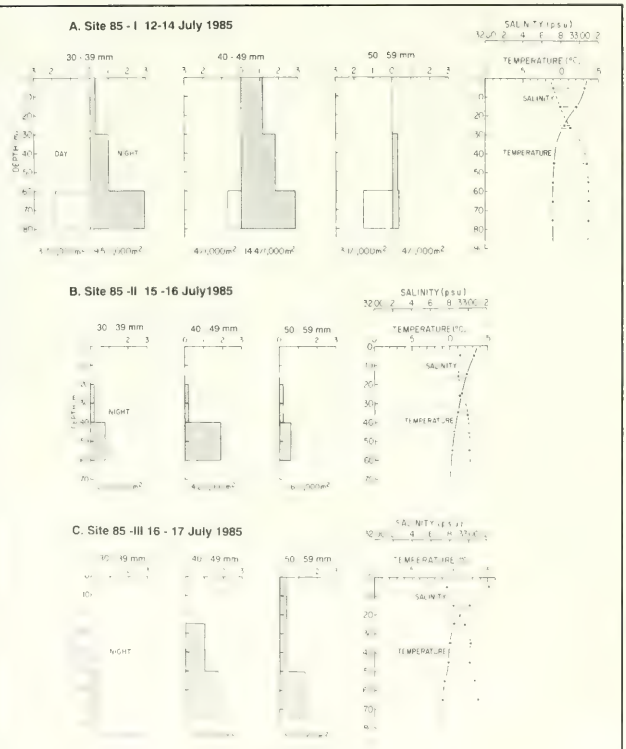

Figure 16

Mean day and night vertical distributions ($\bar{x}$ n/10,000 m^3) of cod *Gadus morhua* size-classes of pelagic juveniles collected by the 10 m^2 MOCNESS on three study sites: **(A)** Site 85-I, stratified, 12–14 July 1985; **(B)** Site 85-II, weakly stratified 15–16 July 1985; **(C)** Site 85-III, stratified, 16–17 July 1985. Estimated water column abundances (n/1000 m^2) are included at bottom of plots. Temperature and salinity profiles are plotted as depth stratum means (●) and 95% confidence limits

was reported by Walford (1938), Colton (1965), and Lough (1984) for haddock on Georges Bank. Their results and other regional studies are reviewed by Frank et al. (1989) and Page et al. (1989) in depth distribution studies of haddock eggs on the Southwestern Scotian Shelf. Because haddock eggs increase their specific gravity with age, newly-hatched larvae were generally found at intermediate depths. Furthermore, these studies found the degree of aggregation for late stage-IV eggs was significantly related to the intensity of stratification.

In the present study, in well-mixed waters during early spring, larval haddock and cod were distributed throughout the water column in the same general pattern as the eggs (Lough 1984), with a mode in abundance at mid-depth, 30–40 m. By mid-May, when the surface water is stratified, larvae resided within the thermocline region; the stronger the stratification, the more closely the abundance centers were confined to the thermocline, especially for the smallest larvae. The larval-thermocline coupling is a dynamic process that is frequently perturbed by strong winds and storms but becomes reestablished with a new thermocline. Even under stratified conditions, larger larvae (>9 mm) tend to be found at greater depths during the day. Day-night shifts in their distribution patterns indicate that diel

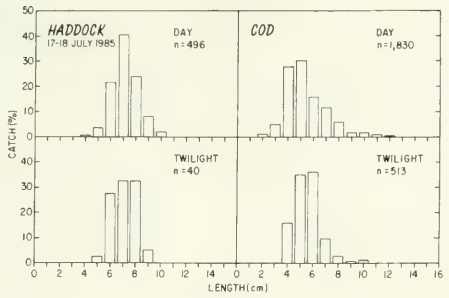

Figure 17

Day and twilight length-frequency distribution of haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* juveniles collected by Yankee 36 bottom trawl on Site 85-IV during a 24 h study, 17–18 July 1985. No fish were caught in night trawls.

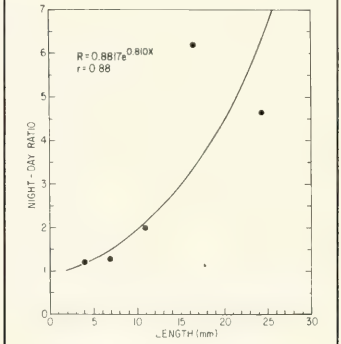

Figure 19

Night-to-day catch ratios for cod, *Gadus morhua*, in tows with 1 m² MOCNESS during April and May 1981 and May 1983. An exponential curve is fitted to the ratios.

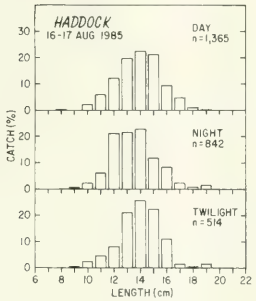

Figure 18

Day, night, and twilight length-frequency distribution of haddock *Melanogrammus aeglefinus* juveniles collected by Yankee 36 bottom trawl on Site 85-V during a 24 h study, 16–17 August 1985.

migrations are fairly well established when larvae reach 9–13 mm length and may be initiated at a smaller size, 6–8 mm, depending on the physical structure of the water column. This pattern of residing deeper by day and shoaler at night continues into the older pelagic juvenile and recently-settled juvenile period.

When larvae reach a length of ~9 mm, the swim bladder may be functionally important in the vertical migration of larvae in both species (Schwartz 1971, Ellertsen et al. 1980, Howell 1984). Haddock and cod have similar developmental patterns; however, there are some important differences (Auditore et al. 1993). At 8–9 mm, haddock have larger and more developed pectoral and pelvic fins than cod. The difference in development is pronounced after 20 mm in length; at 23 mm, the pectoral fins of cod are 1/2 to 3/4 the size of haddock, while the pelvic fins of cod are 1/2 those of haddock. Haddock also possess more total fin rays in the caudal, dorsal, and anal fins than cod. The total number of caudal-fin rays usually determines the overall size of the fin, which is an important means of thrust in gadiform fishes (Cohen 1984). The higher number of caudal- and dorsal-fin rays in haddock, in combination with early paired-fin development, may provide greater maneuverability for haddock. The earlier fin development of haddock larvae compared with cod may allow them to more actively locate high concentrations of prey and stay within these patches. Miller et al. (1963) studied the vertical distribution of larval haddock at three sites on Georges Bank in May 1958. Haddock larvae were found throughout the water column, with maximum concentrations centered at 20–30 m. At all three sites they found periodic changes in the depth distribution of larvae that were related to similar changes in depth of the thermocline. Smaller larvae, 4–8 mm, occurred below the thermocline at each site while >80% of the larger larvae, 9–19 mm, were found in the thermocline. They also found no evidence of diurnal change in the weighted mean depth distribution of larvae, 24 m during the day and 22 m by night. Their observations were in general agreement with those of Frank et al. (1989) for haddock larvae on the Southwestern Scotian Shelf. Frank et al. (1989), using a discrete depth sampler, BIONESS, found recently-hatched haddock larvae in May 1985 and 1986 were concentrated at mid-depth (~30 m) in day and night, and their population centers remained at this level until 20 d post-hatching. The hydrographic conditions were characterized by a density gradient (sigma-*t*) that increased linearly with depth both years. Whereas Miller et al. (1963) and Frank et al. (1989) found had-

dock larvae (<9 mm) below the thermocline, we found both haddock and cod larvae of this size tended to reside mostly within or above the base of the thermocline in May on Georges Bank. Miller et al.'s (1963) ability to discriminate depth changes in larvae was limited because of the small, non-opening/closing samplers (14 cm mouth diameter) that were towed at fixed depth intervals (minimum 9–10 m apart).

Ellertsen et al. (1984) reported on the vertical distribution of cod larvae (4–5 mm) at a strongly-stratified station off the Lofoten Islands, Norway, in May 1982. First-feeding cod larvae were concentrated at 10–20 m depth near the thermocline throughout a 24 h period, but dispersed with the slightest wind mixing. Only under extremely calm conditions were the larvae able to control their vertical distribution and show diurnal migration.

Pelagic juveniles, however, are capable of making extensive migrations through the water column. In our Georges Bank studies, at a well-mixed shoal site in June 1984, pelagic cod juveniles appeared to migrate into the upper half of the water column at night and to remain in the lower water column during the day. Juvenile haddock were much less abundant at this site, and their center of abundance was located at mid-depth with no evidence of day-night migrations like those of cod. The few pelagic cod collected at two stratified sites on eastern Georges Bank in July 1985 were generally found in the lower third of the water column, and few were caught in the thermocline at 15–30 m depth. We have no data on pelagic juvenile haddock at a stratified site for comparison.

Perry & Neilson (1988) studied the vertical distribution of cod and haddock pelagic juveniles in June 1985 on eastern Georges Bank and found a diel migration pattern for both species at a well-mixed shoal site (66 m). At a nearby stratified site in deeper water (80 m), Perry & Neilson (1988) found that juvenile haddock generally remained above 40 m depth with their weighted-mean depth in the thermocline at 20–30 m. In contrast, cod juveniles generally remained deeper than 40 m, below the thermocline, yet still exhibited diel migrations.

Colton (1965) investigated vertical distribution of juvenile haddock using an Isaacs-Kidd midwater trawl in late summer of 1957–58. Over 75% of the pelagic haddock of 27–124 mm occurred between 10 and 40 m depth, with greatest abundance at 20 m at the depth of the thermocline. There was some diel variation in distribution: the weighted-mean abundance was located at 40 m during the day and 30 m at night.

Results from our studies indicate that juvenile haddock and cod change from a pelagic to a demersal existence at a body length of 4–10 cm, and once they reach a demersal stage they stay close to bottom by day and move off bottom into the water column at night. During the transition period the vertical amplitude of these night excursions decreases with size of fish. The data suggest that cod <6 cm make more extensive off-bottom migrations at night than haddock, with some individuals ranging up to the surface. Haddock appear to assume a more complete demersal life at a smaller size (4–6 cm) than cod, which is consistent with older juvenile and adult behavior. Bailey (1975) found that 6.5–13 cm haddock migrated through the water column at night, whereas larger fish were more confined to the seabed in the northern North Sea during August. Beamish (1966) and Woodhead (1966) reported that adult haddock tend to remain associated with the seabed at night, whereas adult cod make extensive vertical migrations. In contrast, Bailey (1975) concluded that cod juveniles remained on or close to the seabed day and night, because fish caught in midwater were never >7 cm, while those on the seabed ranged up to 13 cm.

Juvenile cod and haddock at ~70–90 mm begin feeding on benthic prey such as polychaetes and crustaceans along with planktonic prey, which is consistent with changes in their mouth (Auditore et al. 1993). The time for juvenile cod and haddock to grow from 40 mm to 70 mm is ~30 d, and from 40 to 90 mm is ~48 d (Bolz & Lough 1988). Therefore, in terms of defining the functional transition period for an individual fish, we consider the transition from a wholly pelagic to demersal existence to take ~1–1.5 mo on average.

Other factors influencing vertical distributions

Neilson & Perry (1990) did a recent review of the literature on diel vertical migrations of marine fishes and concluded that the diversity of vertical migration patterns indicated a facultative process significantly influenced by multiple environmental factors. Prey distributions probably play an important role in the vertical distributions of larvae. Based on Georges Bank data (Buckley & Lough 1987) and simulation models (Laurence 1985), haddock larvae are considerably more food-limited than cod. Stable stratified conditions in the spring, which result in the availability of high concentrations of zooplankton prey, favor growth and survival of haddock larvae. Lough (1984) and Buckley & Lough (1987) found that haddock and cod larvae <~13 mm (mode at 7 mm) were generally associated with the planktonic prey biomass that had a maxima in the thermocline during May 1981 and 1983 along the southern margin of Georges Bank. The stronger the water column stratification, the more closely larvae and prey coincided. At the well-mixed sites where larvae were broadly distributed, prey biomass was

lower and more uniformly distributed through the water column.

Frank & McRuer (1989) also found the condition of haddock larvae off Southwestern Nova Scotia in May 1986 consistent with the well-mixed/stratified regime findings of Buckley & Lough (1987). Larvae were in good condition at the deeper stratified sites and in poor condition at the shallow, well-mixed sites. They also found evidence that the buoyancy of starved larvae (4–7 mm) increased, which frequently resulted in a bimodal depth profile, with larvae in poorer condition nearer the surface. Ellertsen et al.'s (1984) study in the Vesteralsfjord of Norway showed that under calm conditions larval cod appeared to concentrate in the surface layers during the night coinciding with the highest density of copepod nauplii, their preferred prey in the study. They also noted that turbulent mixing dispersed the larvae and prey evenly throughout the water column. Therefore, the vertical distribution of larvae and their prey needs to be evaluated in relation to larval buoyancy and water-column turbulence.

Light plays an important role in the diel migrations of cod and haddock larvae, but it is not known whether larvae follow a specific isolume. There may be a critical light intensity at which visual feeding ceases and vertical migration begins. Minimum light-intensity threshold for larval cod feeding was in the range 0.1–0.4 lux, and maximum feeding incidence at 1.4 lux (Ellertsen et al. 1980). Light regime also can affect the swimming activity and buoyancy of yolksac cod larvae by changing their metabolism and utilization of yolk (Solberg & Tilseth 1987).

In Perry & Neilson's (1988) study of pelagic juveniles, the migration pattern of cod appeared to be directly related to the light-dark cycle, whereas that of haddock was more complicated and may have been confounded by periodic changes in the rotary tidal current speed and/or the migratory movements of their preferred mysid prey *Neomysis americana*. Their explanations for the different depth distribution may be related to (1) cod's acclimation to colder waters and haddock's preference for warmer waters, and (2) a possible mechanism for reducing interspecific competition, since their vertical distribution patterns were similar when prey biomass was high and different when prey biomass was low. In our opinion, the differences in vertical distribution between cod and haddock at the stratified site noted by Perry & Neilson (1988) may be attributed to species differences in feeding behavior.

On Georges Bank, planktonic prey selected by both species during settlement at 40–60 mm include copepods, amphipods, euphausiids, and cumaceans (Bowman 1981ab, Koeller et al. 1986, Mahon & Neilson 1987, Lough et al. 1989). Robb (1981) showed that pelagic 0-group gadids in the northern North Sea have a different feeding behavior reflective of the adult lifestyle, i.e., cod fed on larger active pelagic prey, while haddock concentrated on smaller slower-moving or sedentary organisms. Both Robb's (1981) and Perry & Neilson's (1988) feeding results support the view that haddock feed continuously when prey is available.

A complicating factor in understanding vertical distribution patterns in haddock is their commensal association with the large coelenterate *Cyanea* sp. This association has been reported in the literature for fish up to a length of ~10 cm (Colton & Temple 1961, Mansueti 1963, Rees 1966, Bailey 1975, Koeller et al. 1986). Mansueti (1963) stated that jellyfish serve as a source of food and shelter for young fish between the pelagic and demersal stages. The change from a surface to deeper-water habitat by the fish is believed by Mansueti (1963) to be a factor causing the breakup of the commensal relationship. Koeller et al. (1986) showed *Cyanea* sp. to have been most abundant at the surface, decreasing to near zero below 80 m off Nova Scotia in June 1983. Pelagic juvenile haddock, more so than cod, may require contact with some objects such as jellyfish. Whether jellyfish tentacles also serve as a source of food is not known.

The substrate on which the juveniles settle, (i.e., an unsuitable habitat such as sand) may prolong the transition to demersal life. Lough et al. (1989) hypothesized that a large gravel habitat on northeastern Georges Bank favors survival of recently-settled juvenile fish because of predator avoidance through camouflage and/or increased prey abundance. Pelagic juvenile cod were widespread over eastern Georges Bank in June; and in mid-July when they became demersally oriented, they were present on bottom types ranging from sand to gravel. By contrast, in late July to early August, recently-settled juveniles were abundant only on the large gravel deposit on northeastern Georges Bank and were sparse or absent from the large sand and gravelly sand that cover most of eastern Georges Bank (Lough et al. 1989).

To summarize the vertical distribution patterns observed, we developed a generalized day-night mean depth distribution of cod by size-class, from recently-hatched larvae through recently-settled juveniles (Fig. 20). Cod vertical migrations appear to respond primarily to a day-night cycle, whereas haddock migrations respond to other factors such as prey distribution. Depth centers of the smallest larvae (2–8 mm) appear at two levels–15 and 35 m–depending on whether the water column is stratified or well-mixed (Fig. 20). In order for the water column to be considered sufficiently stratified for larvae to initially reside at 15 m, a change of >0.3 sigma-*t* units would have to occur from surface to the base of a pycnocline. Waters around the flank of Georges Bank are typically

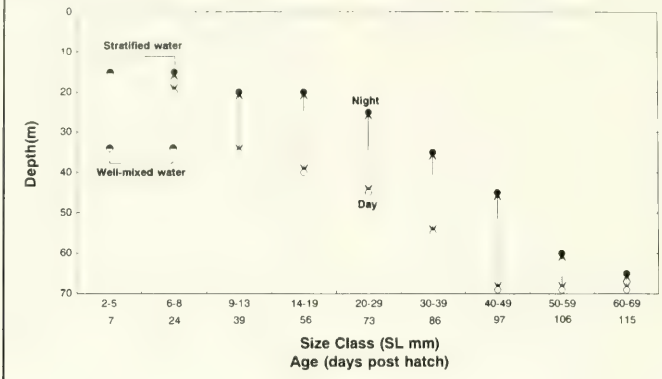

Figure 20

Generalized day-night depth distribution of cod *Gadus morhua* by size-class (mmSL) and age (days post-hatching) from hatched larva through recently-settled juvenile in a 70 m water column. Mean population depth by day (○) and by night (●); vertical range between day and night circles is represented by double arrow. Initial depth centers for the first two size-classes (2–5, 6–8 mm) is largely determined by larval buoyancy and, therefore, whether the water column is well-mixed or stratified.

well-mixed in winter, with a seasonal thermocline developing by mid-May subject to perturbations. When larvae reach a length of 9–13 mm, they appear to make day-night migrations regardless of the water-column structure. There is some uncertainty in the day-night migration range of the pelagic juveniles; however, the 20 m range designated is within their swimming capability at this size. Furthermore, we don't know precisely the transition period from a day to night depth. It probably occurs over a 3–4 h period, but it could be shorter. For example, a 10 mm fish swimming at 1 body length/s could transverse 20 m in 1 h. The vertical distribution pattern presented is sufficiently general to be used as a starting point for both cod and haddock at any bottom depth, even though all situations can be interpreted from the data. These studies highlight the need for investigations of behavior-related sampler avoidance and further time-series of observation on fish distributions in different environmental conditions.

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Table 1

Cruises, sampling sites, and gear used for vertical distribution study on Georges Bank, 1981–86.

Vessel cruise no.	Sampling dates	Site	Bottom depth (m)	Gear	No. depth strata sampled	Tows		
						Night	Day	Twilight
Albatross IV 81-03	27–29 April 1981	81-I	67–70	1m² MOCNESS	6	5	5	0
Albatross IV 81-05	21–27 May 1981	81-II	75–83	1m² MOCNESS	7–8	4	6	0
		81-III	35–58	1m² MOCNESS	7–8	1	3	0
Albatross IV 83-03	13–17 May 1983	83-I	66–79	1m² MOCNESS	7	3	5	0
		83-II	88–93	1m² MOCNESS	8	2	3	0
		83-III	34–54	1m² MOCNESS	5	1	3	0
Albatross IV 84-05	17–19 June 1984	84-I	40–49	10m² MOCNESS	4	3	3	0
Albatross IV 85-06	12–17 July 1985	85-I	80–87	10m² MOCNESS	2–3	4	3	0
		85-II	64–72	10m² MOCNESS	3	3	3	0
		85-III	78–83	10m² MOCNESS	3	2	0	0
Delaware II 85-05	17–18 July 1985	85-IV	80–90	36 Yankee otter trawl with rubber disks	Bottom	1	6	2
Delaware II 85-06	16–17 Aug. 1985	85-V	63–71	36 Yankee otter trawl with rubber disks	Bottom	4	6	2
Albatross IV 86-03	18–22 June 1986	86-I	65–78	10m² MOCNESS	4	5	6	0
	25–26 June 1986			36 Yankee otter trawl with rollers	Bottom	5	11	1

Table 2

Summary of GLM ANOVA for larval haddock and cod abundance on Georges Bank. *F*-values are denoted by their level of significance.

A. 27–29 April 1981 Site 81-I

Factor	Haddock[a]	Cod[b]	Cod[c]	Cod[d]
Depth (D)	3.15*	8.84***	6.50	8.52
Time (T)	2.07	16.59	39.37	50.92
Size (S)		24.68	31.10	29.09***
D × T	0.49	2.03	3.53***	5.31***
D × S		0.28	1.26	0.93
T × S		3.66*	2.33*	0.14
D × T × S		0.68	0.71	0.76

***$P<0.001$
**$P<0.01$
*$P<0.05$

[a]2–5 mm size-class
[b]2–5, 6–8, 9–13 mm size-class
[c]2–5, 6–8, 9–13, 14–19, 20–29 mm size-class
[d]6–8, 9–13, 14–19 mm size-class

B. 24–26 May 1981 Site 81-II

Factor	Haddock[a]	Cod[a]
Depth (D)	6.71	3.76
Time (T)	7.72	9.72
Size (S)	18.17	16.36
D × T	3.52**	2.90*
D × S	0.78	0.33
T × S	1.74	0.69
D × T × S	0.20	0.19

***$P<0.01$

[a]2–5, 6–8, 9–13 mm size-class

C. 13–26 May 1983 Site 83-I Site 83-II

Factor	Haddock[a]	Cod[a]	Haddock[a]	Cod[a]
Depth (D)	4.74	8.17	31.97***	23.84
Time (T)	0.35	0.40	12.11***	0.23
Size (S)	39.67	46.52	15.24***	1.77
D × T	3.13**	0.99	0.86	0.09
D · S	1.25	1.13	1.59	2.29**
T × S	5.33**	0.32	0.13	0.46
D × T × S	1.49	2.31**	1.00	0.93

***$P<0.001$
**$P<0.01$

[a]2–5, 6–8, 9–13 mm size-class

Table 3

Average percentage distribution of haddock and cod larvae in relation to the thermocline at Sites 83-I and 83-II on Georges Bank May 1983. Angular transformation was used on the percentage data: angle = arcsin $\sqrt{\text{proportion}}$. Values are presented as the angular mean ± its standard error followed by a reconverted percentage mean in parentheses.

	Larval size-class					
	2–5 mm		6–8 mm		9–13 mm	
Angle ± SE (%)	Day	Night	Day	Night	Day	Night
A. Site 83-I 13–14 May 1983						
Haddock						
Above thermocline	43.0 ± 12.2 (46.6)	40.7 ± 8.1 (42.6)	22.6 ± 6.4 (14.8)	27.4 ± 9.5 (21.1)	9.9 ± 4.6 (2.9)	25.2 ± 9.5 (18.1)
Within thermocline	32.0 ± 9.3 (28.1)	39.4 ± 4.5 (40.4)	39.5 ± 5.4 (40.5)	49.7 ± 6.2 (58.1)	29.9 ± 4.0 (24.9)	53.4 ± 4.2 (64.4)
Below thermocline	21.7 ± 5.5 (13.6)	22.8 ± 5.8 (15.0)	39.4 ± 6.1 (40.3)	24.9 ± 2.5 (17.7)	56.9 ± 4.8 (70.2)	21.0 ± 5.1 (12.8)
Cod						
Above thermocline	41.0 ± 10.5 (43.0)	29.3 ± 16.9 (23.9)	23.6 ± 6.3 (16.0)	23.5 ± 7.5 (15.9)	6.2 ± 2.8 (1.2)	24.9 ± 2.1 (17.8)
Within thermocline	44.1 ± 14.1 (48.4)	47.5 ± 12.5 (54.4)	45.7 ± 6.9 (51.2)	45.6 ± 4.3 (51.1)	35.8 ± 3.1 (34.3)	46.8 ± 3.4 (53.2)
Below thermocline	18.7 ± 6.4 (10.3)	22.0 ± 3.5 (14.1)	32.6 ± 5.5 (29.1)	39.7 ± 4.8 (40.7)	53.1 ± 3.2 (63.9)	32.0 ± 5.2 (28.1)
B. Site 83-II 15–16 May 1983						
Haddock						
Above thermocline	31.3 ± 2.5 (27.4)	48.0 ± 14.5 (55.1)	23.7 ± 7.3 (16.1)	34.1 ± 9.1 (31.4)	12.1 ± 5.2 (4.4)	31.9 ± 12.3 (27.9)
Within thermocline	58.4 ± 2.4 (72.5)	42.1 ± 14.5 (44.9)	64.8 ± 6.5 (81.9)	55.7 ± 8.9 (68.2)	60.5 ± 2.8 (75.7)	56.0 ± 11.1 (68.7)
Below thermocline	3.5 ± 1.7 (0.1)	1.8 ± 0.0 (0.1)	6.6 ± 1.7 (1.3)	3.1 ± 1.3 (0.3)	21.0 ± 8.0 (12.8)	9.4 ± 2.4 (2.6)
Cod						
Above thermocline	35.6 ± 6.7 (33.9)	33.6 ± 4.7 (30.5)	20.9 ± 1.9 (12.7)	27.2 ± 3.1 (20.9)	1.8 ± 0.0 (0.1)	18.1 ± 16.3 (9.6)
Within thermocline	54.5 ± 6.7 (66.1)	45.0 ± 10.1 (50.0)	69.2 ± 1.9 (87.4)	62.8 ± 3.1 (79.1)	63.6 ± 5.5 (80.3)	72.9 ± 17.1 (91.3)
Below thermocline	8.1 ± 0.0 (0.1)	1.8 ± 0.0 (0.1)	1.8 ± 0.0 (0.1)	1.8 ± 0.0 (0.1)	26.4 ± 5.5 (19.7)	1.8 ± 0.0 (0.1)

Table 4

Summary of GLM ANOVA for juvenile haddock and cod abundance on Georges Bank. *F*-values are denoted by their level of significance.

A. 17–29 June 1984	Site 84-I			
Factor	Haddock[a]	Haddock[b]	Cod[c]	Cod[d]
Depth (D)	1.12	0.59	0.24	0.04
Time (T)	0.48	0.53	0.12	0.06
Size (S)	11.60***		11.46**	0.34
D × T	1.23	0.46	0.34	0.11
D × S	0.37		0.10	0.03
T × S	0.26		0.49	0.02
D × T × S	0.48		0.09	0.03

***$P<0.001$
**$P<0.01$
*$P<0.05$

[a]9–13, 14–19, 20–29 mm size-class
[b]14–19 mm size-class
[c]14–19, 20–29, 30–39 mm size-class
[d]14–19, 20–29 mm size-class

B. 18–22 June 1986	Site 86-I
Factor	Cod[a]
Depth (D)	41.78***
Time (T)	9.98*
Size (S)	4.76*
D × T	0.65
D × S	1.09
T × S	1.91
D × T × S	0.30

***$P<0.001$
**$P<0.01$
*$P<0.05$

[a]20–29, 30–39 mm size-class

Table 5

Number and size of juvenile cod (3–9 cm) collected by time of day in bottom trawls, Site 86-I, 25–26 June 1986, *ALBATROSS IV* 86-03.

	No. trawls	$\bar{x}$ *n*/trawl	SD	CV %	$\bar{x}$ length (cm)	SD	Total no. fish
Night	5	102.8	52.7	51	4.2	0.45	513
Day	11	2.9	1.3	45	4.8	1.48	32
Twilight	1	6.0	—	—	4.4	1.27	6

Table 6

Number and size of juvenile haddock (4–10 cm) and cod (2–12 cm) collected by time of day in bottom trawls, Site 85-IV, 17–18 July 1985, *DELAWARE II* 85-05.

	No. trawls	$\bar{x}$ *n*/trawl	SD	CV %	$\bar{x}$ length (cm)	SD	Total no. fish
Haddock							
Night	1	1.0	—	—	9.0		1
Day	6	84.8	64.6	76	7.1	1.1	496
Twilight	2	20.0	9.9	50	7.1	1.0	40
Cod							
Night	1	—	—	—	—	—	—
Day	6	305.0	391.3	128	5.4	1.6	1,830
Twilight	2	256.6	244.0	95	5.5	1.1	513

Table 7

Number and size of juvenile haddock (3–19 cm) collected by time of day in bottom trawls, Site 85-V, 16–17 August 1985, *DELAWARE II* 85-06.

	No. trawls	$\bar{x}$ *n*/trawl	SD	CV %	$\bar{x}$ length (cm)	SD	Total no. fish
Night	4	210.5	143.6	68	13.9	1.68	842
Day	6	227.5	114.4	50	13.5	1.76	1,365
Twilight	2	257.0	4.2	2	14.0	1.68	514

Table 8

Night/day abundance ratios (n/10 m^2) for cod and haddock by length size-classes using the 1 m^2 MOCNESS, April and May 1981 and May 1983.

Size-class (mm)	April 1981 Site 81-I	May 1981 Site 81-II	May 1983 Site 83-I	May 1983 Site 83-II	Total	Ratio
Cod						
2–5	37/28	16/7	7.4/7.5	7/13	67.4/55.5	1.21
6–8	30/14	58/35	37/47	13/14	138/110	1.26
9–13	213/98	7/8	16/12	5/4	241/122	1.98
14–19	62/10				62/10	6.20
20–29	14/3				14/3	4.67
Haddock						
2–5	108/66	250/143	93/43	10/55	461/307	1.50
6–8	0.6/1.8	483/473	354/468	168/236	1006/1179	0.85
9–13		66/119	123/189	67/59	256/367	0.70

Table 9

Night/day abundance ratios (n/1000 m^2) for cod and haddock by length size-classes using the 10 m^2 MOCNESS, June 1984, June 1986, and July 1985.

Size-class (mm)	June 1984 Site 84-I	June 1986 Site 86-I	July 1985 Site 85-I	Total	Ratio
Cod					
9–13	0.3/2.5			0.3/2.5	0.12
14–19	54/29	6.4/2.7		60.4/31.7	1.91
20–29	170/45	134/79		304/124	2.45
30–39	5/0.5	154/110	9.5/3.7	168.5/113.5	1.49
40–49		8.5/6.12	14.4/1.4	22.9/7.5	3.05
50–59			1.4/3.1	1.4/3.1	0.45
Haddock					
9–13	4/9			4/9	0.44
14–19	20/16			20/16	3.33
20–29	4/0.9			4/0.9	4.44

Abstract.—Line transects run from a manned submersible were used to estimate the current density of yelloweye rockfish in two areas of the eastern Gulf of Alaska. Yelloweye rockfish were seen in cobble, continuous rock, broken rock, and boulder habitats but were most abundant in broken rock and boulder habitats. The presence of refuge spaces appears to be an important factor affecting occurrence of yelloweye rockfish. Boulder areas in deep water (>108 m) were the most densely-populated habitat, with an estimated density of 9135 adult yelloweye/km^2. Overall density by area and year ranged from 1954 to 2217 adult yelloweye rockfish/km^2. Habitat-specific density estimates were less precise than general area estimates because of smaller sample sizes. For fisheries management, density estimates may be extrapolated to larger areas based on areal estimation of yelloweye habitat from available bathymetric data.

Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska*

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The yelloweye rockfish *Sebastes ruberrimus* is the target species of the commercial longline fishery for Demersal Shelf Rockfishes (DSR) in the eastern Gulf of Alaska (O'Connell & Fujioka 1991). Rockfishes (*Sebastes* spp.) are managed on an assemblage basis in the Gulf of Alaska under the advice of the North Pacific Fishery Management Council (NPFMC). Demersal Shelf Rockfishes comprise eight species of bottom-dwelling rockfishes inhabiting rocky areas of the continental shelf; yelloweye rockfish account for 96% of the landed catch of targeted DSR.

Traditional stock-assessment methods are difficult to apply to DSR because of a combination of behavioral and physiological factors. The close association of DSR with rugged bottom precludes the use of bottom-trawl surveys used for assessing other groundfish in the Gulf of Alaska. Mark-recapture studies are also ineffective because rockfishes incur high embolism mortality when brought to the surface from depth (O'Connell 1991). Consequently, prior to our research, DSR was one of only two assemblages managed under the Gulf of Alaska Fisheries Management Plan for which no biomass estimates were available.

It has been well documented that rockfish tend to be habitat-specific in their distribution (Love & Ebeling 1978, Larson 1980, Richards 1986, Matthews 1991, Love et al. 1991, Matthews & Richards 1991, Rosenthal et al. 1982). Therefore, to estimate their abundance, we initiated a project designed to take advantage of the preference by DSR for rough, rocky habitat. Our approach was based on the assumption that DSR abundance increases with structural habitat complexity (i.e., increased topographic relief and more interstitial space in and between rocks). Our objective was to estimate density of yelloweye rockfish in the Gulf of Alaska for selected habitat and depth categories. We hope to eventually develop a model predicting the relationship between DSR abundance and habitat complexity and to use this model to indirectly estimate the abundance of DSR. If successful, this approach would allow for expansion of abundance estimates to other areas in the eastern Gulf of Alaska without replicating costly surveys.

Methods

Using the submersible *Delta*, we made 20 dives and covered 47 transects during 17–25 August 1990 in two areas off southeastern Alaska (Fig. 1).

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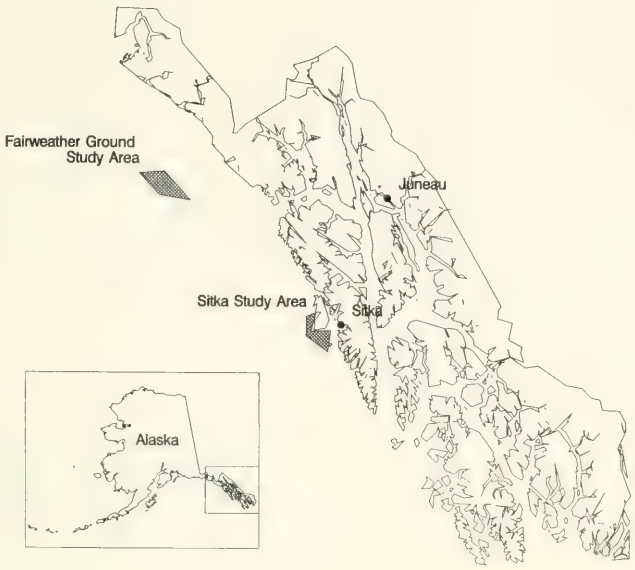

Figure 1

Study sites for submersible survey of yelloweye rockfish, eastern Gulf of Alaska, 1990–1991.

Eleven dives were made on the Fairweather Ground and nine dives were made off Sitka Sound. Eighteen dives and 30 transects were completed off Sitka Sound during 27 May–3 June 1991. One transect was replicated at night to compare day and night effects. Transect locations were chosen systematically to include sites with a range of topographical relief. Bathymetric data from the National Ocean Service Hydrographic and Marine Geophysical databases were used as an aid in site location.

In a typical dive in 1990, three transects were run per dive with each transect lasting 30 min. In 1991, transect durations were extended to 1 h with two transects run per dive. *Delta*'s pilot attempted to maintain a constant speed of 0.5 kn and to remain within 1m of the bottom, terrain permitting. A predetermined compass heading was used to maintain position along a transect line. Periodic locational fixes of *Delta* along each transect were recorded using a TRAK-POINT navigation system aboard the support vessel, in combination with a Loran (1990) or a global positioning system (1991). The length of each transect (l_i) was measured as the sum of distances between locational fixes.

The usual procedure for line-transect sampling entails counting objects on both sides of a transect line. Due to the configuration of the submersible, we only counted fish on the right side of each line. Horizontal visibility was usually good, 5–15 m. All fish observed from the starboard port were individually counted and their perpendicular distance from the line recorded (Buckland 1985). The observer used the lower and middle starboard ports for viewing. An externally-mounted video camera was used to record both habitat and audio observations of species encountered and perpendicular distances to fish. Yelloweye rockfish have distinct coloration differences between juveniles and adults, so observations of the two were recorded separately, and also on a back-up tape recorder. A Pisces Box data-logger recorded depth of the submersible and its distance from the bottom, time of day, and temperature onto the videotape at 1s intervals. These data were later downloaded onto a microcomputer spreadsheet. In addition to the video system, we used a Photosea 35 mm camera with strobe to photograph habitat and fish. Two lamps were mounted externally to provide lighting for the camera systems.

Hand-held sonars were modified to obtain perpendicular distance recordings. Two sonar models were used: Manta and Scubapro. The end of each gun was fit with a tight (rubber) reservoir cinched to the sonar barrel. The reservoir was filled with water, and a syringe used to remove air bubbles. The end of the reservoir was kept damp by resting it on a wet sponge. A digital read-out of the distance from the submersible to its target was obtained by pressing the reservoir end of the gun against the port, aiming the gun, and pressing the trigger. To verify the accuracy of this method, we confirmed readings by positioning a scuba diver at intervals along a marked transect line.

Six habitat categories were used: soft, gravel, cobble, continuous rock, boulder, and broken rock. Other descriptions of habitat were also recorded, including rock type (e.g., basalt), invertebrate cover, and vertical relief. To analyze depth differences, two depth intervals were defined: shallow <108 m, and deep ≥108 m.

Density estimates were obtained for combinations of species, area, depth, and habitat type using the density estimator advanced by Burnham et al. (1980), except that length of transect (l_i) as used in the denominator was not doubled, since we were able to count fishes only on one side of each line transect. Data from all transects were combined, and yelloweye rockfish density was estimated as

$$\hat{D}_{YE} = \frac{n\hat{f}(0)}{L},$$

where n = total yelloweye rockfish adults observed (from all transects), and L = total line length (all transects combined) in meters.

We used the indirect method of estimating variance in density (Burnham et al. 1980:54), and $f(0)$ was estimated from detection functions based on the hazard-rate perpendicular distance model of Hayes & Buckland (1983).

Results

Density estimates

No discernable difference was noted in the occurrence of yelloweye rockfish between day and night replicate transects, and all density estimates are calculated from daytime dives. Estimated densities of yelloweye rockfish in 1990 and 1991 varied from 1954/km^2 to 2531/km^2 (Table 1). Estimated probability density functions (pdf) generally exhibited the "shoulder" (i.e., an inflection and asymptote in the pdf for perpendicular distances near 0) that Burnham et al. (1980) discuss as a desirable attribute of the pdf for estimation of f(0) (Fig. 2).

Habitat effects

Boulder fields were the most densely populated habitat type, followed by broken rock (Table 2). Although density was greater in boulder cover regions, the occurrence of this habitat type was relatively infrequent, accounting for only 16% of the total bottom surveyed.

Surveyed habitat ranged from low-relief mud to high-relief pinnacles and cliff faces. The predominant rock type was volcanic, including folded lava flats and columnar basalt. Adult yelloweye rockfish were encountered over all habitats surveyed, but occurred most frequently over broken rock and boulder fields, often observed resting in refuge spaces such as cracks, caves, or overhangs (Fig. 3). They were also observed hovering off cliff faces above cobble or pavement bottoms. Generally, only one yelloweye rockfish was observed per refuge space, but often the hole was co-occupied by a tiger rockfish *Sebastes nigrocinctus*. Frequency-of-occurrence of yelloweye rockfish over soft, cobble, and continuous rock bottom was too low to provide acceptable line-transect density estimates. In both the Sitka Sound and Fairweather areas, there are infrequent abrupt pinnacles overlaid with massive boulders and overhangs. Density of yelloweye and other species was extremely high in these habitats. In the Sitka area we surveyed two adjacent pinnacles: one pinnacle highly dissected with many boulders and overhangs, the other comparatively smooth. Occurrence of yelloweye rockfish on the complex habitat pinnacle was clearly higher than on the smoother pinnacle. Alhough gross vertical relief is similar between the two pinnacles, the number of refuge spaces differed and appeared to be important in the occurrence of yelloweye rockfish.

Table 1
Density estimates, CV(D), and 95% CL for adult yelloweye rockfish by area and year.

Year/Area	Density no./km^2	n	CV(D)	95% CL Lower	95% CL Upper
1990 Fairweather	2217	221	19.5	1184	3250
1990 Sitka	1954	236	25.3	813	3054
1991 Sitka	2065	352	14.9	1347	3165

Depth effects

Depth effects on abundance were difficult to interpret because of the confounding influence of habitat. Depth-related density differences were evaluated by combining the 1990 and 1991 Sitka data and examining two depth zones within the two preferred habitat types: broken rock and boulder. In both habitats, deep zones had higher abundances than shallow zones within the same habitat type. Boulder areas differed the most between shallow and deep zones: The highest estimated density in boulder areas was in the deep zone where 9135 yelloweye rockfish/km^2 were counted, compared with 6122 yelloweye rockfish/km^2 in the shallow zone. The deep-zone broken-rock habitat had 2831 yelloweye rockfish/km^2, compared with 2748/km^2 for the shallow zone.

Juvenile yelloweye

Abundance of juvenile yelloweye rockfish was too low to obtain reliable habitat-specific density es-

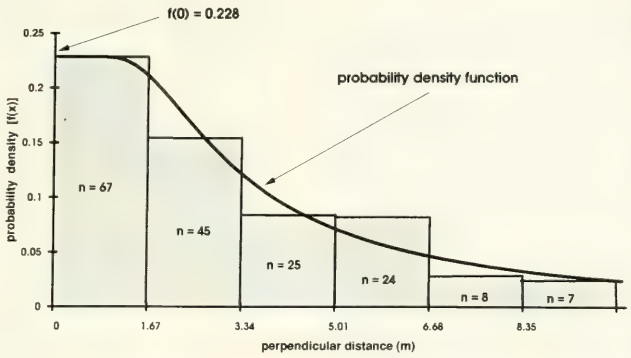

Figure 2

Representative probability density function (pdf) and histogram of relative frequencies ($n_i/(\Delta_i n)$) of yelloweye rockfish observed for 5 distance intervals over boulder habitat in the Sitka study area, 1990. For relative frequencies, n_i = number of fish observed in interval i, Δ_i = size of class interval (in this case, 1.67m), and n = total number of yelloweye observed (in this case, 176).

timates; hence they varied considerably (Table 3). Data on frequency-of-occurrence/meter traversed suggested preference by juvenile yelloweye rockfish for the shallow-zone broken-rock habitat.

Discussion

In addition to confirming the strong association of yelloweye rockfish with rocky habitat noted by Richards (1986), we were able to estimate overall and habitat-specific densities for yelloweye rockfish. The only previously published estimates of yelloweye rockfish densities are from the Strait of Georgia, British Columbia. Richards (1986) used strip transects conducted from the submersible *Pisces VI* to describe spatial distribution patterns of rockfish. Although our results were not directly comparable to hers because of differences in habitat categorization and because juvenile yelloweye rockfish were included in her density estimates, our results were similar. For two depth categories, 21–80 m and 81–140 m, Richards (1986) estimated yelloweye rockfish densities of ~10,000 and 14,000 yelloweye/km^2 in her complex habitat category, including high-relief areas of cobble with large rock, broken rock, and boulder, a category that may encompass our broken-rock and boulder habitat types. In our study, estimated densities in boulder and broken-rock habitats varied from 2405 to 9135 yelloweye rockfish/km^2 depending on depth. Comparison of estimated densities from roughly similar habitat types in the two studies suggests that yelloweye densities in the Strait of Georgia, BC were greater than we estimated for the coast of southeast Alaska.

Use of the submersible allowed collection of qualitative data for assessment of factors contributing to the distribution and abundance of fishes. Occurrence of refuge spaces may be one key to the presence of yelloweye rockfish, which were normally in areas where refuge spaces were available, even if the surrounding habitat was not the preferred habitat of boulder or broken rock. For example, we often encountered yelloweye rockfish under overhangs of large, solitary boulders in cobble flats. Continuous rock bottom was not particularly good habitat in terms of yelloweye density. Additional transects will be needed to increase the precision of habitat-specific estimates and narrow the associated confidence limits. Further refinement of habitat categories (e.g., subcategories of boulders based on average size of boulders and/or interstitial spaces) may also yield more precise habitat-specific estimates for yelloweye.

Differences in density estimates for juvenile yelloweye between the Fairweather and Sitka sites are interesting. The higher density on the Fairweather site may be due to terrain: the Fairweather Ground is a well-defined bank surrounded by large ex-

Table 2

Density estimates for adult yelloweye rockfish by habitat category, area, and year.

Habitat	Year/Area	n	Density no./km^2	CV(D)	95% CL Lower	95% CL Upper
Boulder	1990 Fairweather	59	3660	36.60	792.2	6527.1
	1990 Sitka	52	3712	53.70	0	8015.8
	1991 Sitka	82	5026	30.99	1693.0	8358.9
Broken rock	1990 Fairweather	143	3312	24.50	1575.1	5048.8
	1990 Sitka	175	2515	20.80	1393.2	3637.6
	1991 Sitka	253	2405	40.81	304.84	4505.16

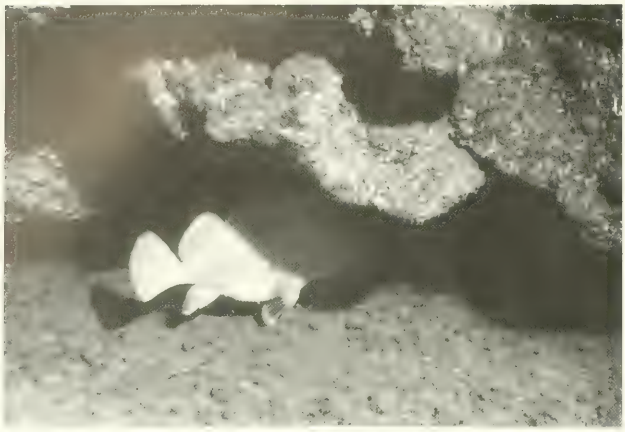

Figure 3
An adult yelloweye rockfish in a typical "refuge space."

Table 3
Density estimates for juvenile yelloweye rockfish by area, eastern Gulf of Alaska, 1990.

Area	Density n	no./km^2	CV(D)	95% CL Lower	95% CL Upper
Fairweather	140	1766	21.34	959.2	2572.7
Sitka	48	497	40.77	63.3	929.7

panses of soft bottom. This topography may cause juveniles to be more closely aggregated than in the Sitka area, where reefs and pinnacles are often linked by hard bottom, e.g., continuous lava flats. Although hard bottom is not ideal habitat, it may promote movement of fish between reefs.

Our ultimate goal is to develop a quantitative predictive model to estimate density of yelloweye rockfish and other DSR species based on one or more parameters reflective of structural habitat complexity. In the interim, the use of line transect-derived density estimates can be directly applied in fisheries management. In the absence of a fishery-independent biomass estimate, the total allowable catch (TAC) currently in use for demersal shelf rockfish had previously been based on historical catch information. In contrast, the transect data allowed us to estimate biomass/km^2 and to expand this estimate to a larger area using an estimate of area of rocky habitat inside the 180 m deep edge of the continental shelf. Allowable biological catch (ABC) and TAC can then be set, using known life-history information including estimates of natural mortality. In 1991, the Gulf of Alaska Plan Team of the NPFMC used this approach in recommending an ABC for the demersal shelf rockfish assemblage in the East Yakutat District (O'Connell et al. 1991).

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Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: Northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus**

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Abstract.—We describe a simple biostatistical model of reproductive success (logarithm of recruits/spawner) applied to three coastal pelagic fish stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus*. We used the model to detect possible influences of gross climatic conditions and contaminant loadings (particularly of metals and organochlorines) on reproduction in these three stocks. Data included several decades of annual estimates of recruitment and stock size, monthly measures of climate, and annual estimates of contaminant loadings; the model included a compensatory stock-size component before adding environmental effects. The study was meant to generate, rather than test, hypotheses. For the chub mackerel stock, we detected climate influences, but no contaminant influences, on reproductive success, which was usually high during conditions typical of El Niño–Southern Oscillation events. For the northern anchovy stock, we detected no climate or contaminant influences on spawning success; however, the negative results may reflect low statistical power, rather than absence of contaminant influences. For spawning success in the Pacific sardine stock, we detected no consistent climate influences, but we found a strong negative correlation with contaminant loadings. This result is consistent with the hypothesis that contaminant loadings accelerated the collapse of the Pacific sardine stock while it was under stress from severe overfishing. Although many scientific questions about validation of models, mechanisms of action, and identity of specific deleterious contaminants remain to be answered, the observed data are well described by the hypothesis of contaminant-mediated decline.

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In recent years, there has been increasing concern about possible effects of contaminants on the nation's living resources, particularly exploited fish and shellfish populations. Although contaminants such as heavy metals and synthetic organochlorines are commonly detectable in coastal sediments, waters, and organisms (Mearns et al. 1991), it has been difficult, if not impossible, to determine whether sublethal levels of contaminants have influenced the productivity of coastal fish stocks. Mass mortalities and deformities of fish and shellfish have occurred after exposure to high levels of contaminants, but mortality and morbidity in natural populations attributed to chronic low-level exposures is difficult to prove conclusively, even though it may be strongly supported by circumstantial evidence (Sindermann 1978).

In addition, the question of population-level effects has been largely unexplored. For individuals of most species, the physiological effects (if any) of chronic sublethal exposure to contaminants are poorly understood. For populations, the effects of such exposure are not known. Nonetheless, evidence from many studies of individuals suggests that populations should be affected also.

This paper describes exploratory models of the effects of contaminants, climate, and spawning-stock size on three exploited fish populations off southern California. With a rich body of data, this area is unusually well suited to such a study. The waters off southern California contain elevated levels of numerous contaminants, including PCBs, DDT, and several toxic metals (McCain et al. 1988). Estimates of historical contaminant loadings have been made by Summers et al. (1988), and data on climatic conditions are available from public records. Major coastal pelagic fisheries have been monitored by the California Department of Fish and Game since about 1930.

Two main conceptual approaches might be used to model the effects of contaminant exposure on populations. The first approach is a "bottom-up" one: constructing a

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mechanistic population model that somehow extrapolates known effects on individual organisms to effects at the population level. The second approach is entirely at the population level: construction of statistical models that correlate historical changes in population properties (especially properties thought to be sensitive to environmental fluctuation) to changes in contaminant loadings.

Neither of these approaches is completely satisfactory. Weighing against the first approach is the fact that the existing theory of population biology does not allow extrapolation from physiology and behavior of individuals to the net productivity of the population. Indeed, biological populations seem to have emergent properties unknowable from the observable properties of individuals (Mayr 1982). A similar problem is that combinations of contaminants may work in unforeseen ways; one might say that such combinations have their own emergent properties. Thus the biological activity and availability of mixtures of contaminants in the coastal environment are difficult, if not impossible, to extrapolate from laboratory studies of exposure to individual contaminants. Given the seemingly insurmountable barriers to constructing mechanistic bottom-up models of populations chronically exposed to low levels of contaminants, we used the alternative approach: we constructed empirical statistical models of contaminant effects on populations. The empirical approach, of course, also has many limitations; these are discussed at length in later sections.

Model structure

Evidence suggests that the youngest stages of fishes should be most sensitive to the effects of contaminants (Weis & Weis 1989). For that reason, our model of contaminant effects addresses survival from the egg stage to age of recruitment (roughly the first year of life). The model is based on the widely-used Ricker (1954) model of fish recruitment:

$$R = \alpha P e^{\beta P} \zeta, \qquad (1)$$

where R = recruitment in number of fish or biomass,
P = parent spawning-stock size (usually spawning biomass),
α, β = estimated parameters of the Ricker model,
e = base of natural logarithms, and
ζ = a lognormally-distributed stochastic component with zero mean.

A common interpretation of Eq. 1 is that α represents the net fecundity of a unit of spawning biomass and β reflects the degree of density-dependence in the stock's recruitment.

The Ricker model is often expressed in terms of the natural logarithm of recruits per spawner:

$$\log(R/P) = a + bP + \varepsilon, \qquad (2)$$

where $a = \log(\alpha)$, $b = -\beta$, and $\varepsilon = \log(\zeta)$. (The sign change in b is made merely to simplify the notation; b is negative in a compensatory stock.) Assuming that the total number of eggs spawned is proportional to the spawning biomass P, the quantity R/P is an index of an egg's probability of survival to recruitment. This seems to be a more appropriate quantity to use for detecting exogenous effects than recruitment itself, which is usually held to depend in the first order upon stock size. We refer to the quantity R/P as "spawning success" and to its natural logarithm as "log spawning success." The model of log spawning success (Eq. 2) is linear in the parameters and contains an additive error structure, and thus can be fit by ordinary least-squares (OLS) regression.

Eq. 2 can easily be modified to incorporate external variables, such as climate or contaminant effects, that might affect spawning success. Suppose we have m such variables, $\{x_1, x_2, \ldots, x_m\}$, for which we wish to estimate parameters $\{\theta_1, \theta_2, \ldots, \theta_m\}$. Then a model including these variables is

$$\log(R/P) = a + bP + \sum_{i=1}^{m} \theta_i x_i + \varepsilon. \qquad (3)$$

In this expanded model, m explanatory variables and population size affect log spawning success in an additive manner. The application of this linearized model is described in a later section. Other adaptations of the Ricker model to represent contaminant effects were made by Goodyear (1983) and Vaughan et al. (1984).

Data sources and processing

Two main categories of data were used in this study: data on fish abundances, and explanatory data on the environment. Data on fish populations comprised time-series of age-structured abundance estimates from virtual population analyses (VPA). We examined three coastal pelagic stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus* (known locally as Pacific mackerel).

These stocks were chosen because they have each supported major fisheries and have been studied sufficiently well so that long time-series of stock and recruitment data are available. These coastal pelagic species also form a conspicuous part of the California Current ecosystem.

Explanatory data (data on the environment) included time-series of two types: variables related to climate, and variables reflecting contaminant loadings or other potential human impacts. These data were subjected to a number of stages of preliminary processing, including two principal component analyses, to compute two sets of derived variables (principal components) from a larger number of potential explanatory variables.

Data on fish abundances

Stock and recruitment data on northern anchovy (Table 1, Fig. 1) were obtained from Table 8 of Methot (1989), who derived his estimates from fishery statistics and research survey data. For spawning-stock size, we used

Table 1

Stock and recruitment data used for modeling effects of contaminants and climate on spawning success of three pelagic fish stocks off southern California. Data on chub mackerel have traditionally been reported, maintained, and analyzed in the English system, and are so reported here.

	Northern anchovy *Engraulis mordax*		Pacific sardine *Sardinax sagax*		Chub mackerel *Scomber japonicus*	
Year	Spawning biomass 10^6t	Recruitment 10^9 fish	Spawning biomass 10^3t	Recruitment 10^6 fish	Spawning biomass 10^6 lbs	Recruitment 10^6 lbs
1946	—	—	566	3875	97.87	20.11
1947	—	—	405	4261	57.91	139.20
1948	—	—	740	3690	28.90	70.92
1949	—	—	793	290	72.43	11.21
1950	—	—	780	397	89.46	3.59
1951	—	—	277	972	72.05	3.80
1952	—	—	136	1197	32.89	55.35
1953	—	—	202	382	10.62	106.48
1954	—	—	239	264	38.58	45.90
1955	—	—	170	588	80.69	91.41
1956	—	—	108	1586	95.00	20.05
1957	—	—	90	905	77.30	28.00
1958	—	—	177	288	36.98	91.81
1959	—	—	122	111	33.59	70.18
1960	—	—	88	74	63.02	128.67
1961	—	—	54	56	81.32	85.60
1962	—	—	27	11	133.10	18.18
1963	—	—	—	—	168.65	9.58
1964	639,210	38.6	—	—	112.05	2.67
1965	531,520	13.4	—	—	44.27	4.21
1966	541,880	13.3	—	—	17.63	5.75
1967	409,170	27.9	—	—	4.11	1.14
1968	396,260	19.8	—	—	2.57	4.08
1969	374,300	33.1	—	—	—	—
1970	321,880	73.1	—	—	—	—
1971	333,600	123.3	—	—	—	—
1972	588,460	154.2	—	—	—	—
1973	1,812,900	114.9	—	—	—	—
1974	1,481,160	32.6	—	—	—	10.15
1975	1,458,430	14.3	—	—	0.63	2.53
1976	1,050,180	57.2	—	—	5.00	138.43
1977	868,890	6.5	—	—	22.68	89.87
1978	435,370	114.3	—	—	95.06	252.20
1979	582,890	82.0	—	—	166.36	35.40
1980	798,280	74.0	—	—	255.27	185.41
1981	782,770	19.7	—	—	332.28	158.58

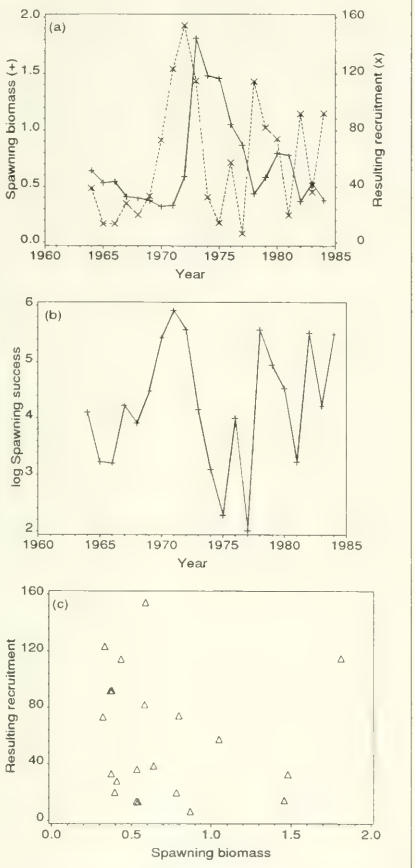

Figure 1

Recruitment of the northern anchovy *Engraulis mordax* stock off southern California. **(a)** Time trajectories of recruitment R (10^9 fish) and spawning biomass P (10^6t); **(b)** time trajectory of log (R/P); **(c)** stock-recruitment scatterplot, in same units as (a).

Methot's estimates of spawning biomass on 15 February of each year. For recruitment, we used Methot's estimates of the number of recruits on 1 July of the same year. Methot stated that his estimates of recruitments before 1964 are much less precise; we used his estimates of 1964 through 81 (the end of the contaminant data series).

Stock and recruitment data on Pacific sardine (Table 1, Fig. 2) are the estimates of MacCall (1979, Table 3), and were derived from fishery statistics. Although the estimates extend through 1964, MacCall (1979) discounted the 1963 and 1964 estimates of recruitment as not sufficiently precise. We used the estimates from 1946 (the beginning of the contaminant series) through 1962.

Stock and recruitment data on chub mackerel (Table 1, Fig. 3) are from Table 1 of Prager & Hoenig (1989), who compiled data from MacCall et al. (1985), Parrish & MacCall (1978), and Prager & MacCall (1988a). The estimates, all derived from fishery statistics, were adjusted by Prager & Hoenig (1989) to a common reporting date. The temporal limits of our analysis, 1946–81, were determined by the limits of the contaminant series. The chub mackerel data span a stock collapse and subsequent closure of the fishery and thus have 6 yr (1969–74) of data missing. Nonetheless, the chub mackerel series (n=30) is the longest of the three stocks. The data encompass at least two distinct epochs in the existence of the population: the pre-collapse epoch of steadily increasing exploitation rate, and the post-collapse epoch of more strictly regulated fishing and the associated population increase.

Explanatory data: Contaminants

Historical contaminant-loadings data were compiled and reconstructed by Summers et al. (1988) according to a mass-balance approach based on manufacturing volume, land use practices, and mobility of particular contaminants. Summers et al. (1988) also compiled more general measures (e.g., wastewater flow) from governmental records. The resulting annual time-series include five major categories: gross indicators, physical-biological factors, nutrient loadings, organochlorine loadings, and metal loadings (Table 2). Prager & MacCall (1990) discussed the loading patterns of individual contaminants and provided time-series plots of each; here, we review major characteristics abstracted from Summers et al. (1988) and Prager & MacCall (1990).

The human population of southern California has increased sharply over the last 50 yr, and this is reflected in many contaminant-loading patterns, particularly in the first three categories (Table 2). For example, loadings of nitrogen, phosphorus, and total organic carbon arise principally from wastewater (sewage) flow, which has increased with population size; power-plant cooling flows, for the most part, also reflect the growing population's use of electricity. While size of the annual kelp harvest is strongly correlated with human population size, the relationship may be noncausal; this is impossible to ascertain statistically. Nonetheless, size of the kelp harvest was included among other potential indicators of environmental stress, as many species are present in kelp-forest habitat during early stages of life history.

With the exception of PCBs, the organochlorines listed in Table 2 were all introduced in the late 1940s. Most fluctuations in individual loadings have followed legal restrictions on use (e.g., of DDT) and subsequent increased use of

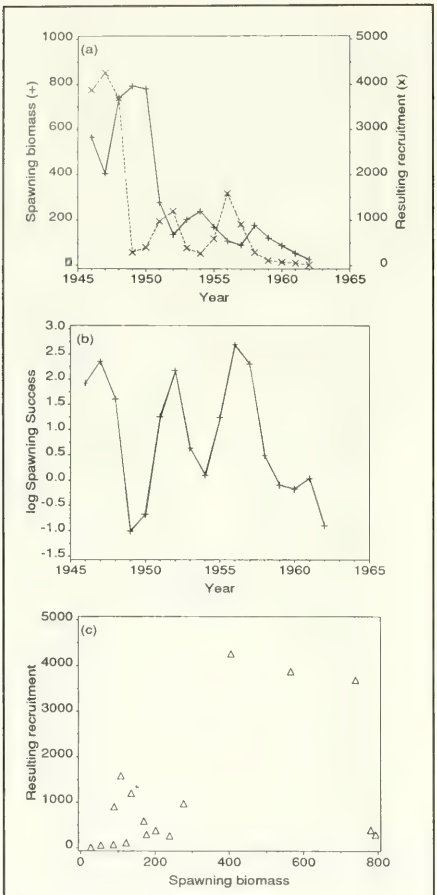

Figure 2

Recruitment of the Pacific sardine *Sardinops sagax* stock off southern California. **(a)** Time trajectories of recruitment R (10^6 fish) and spawning biomass P (10^6t); **(b)** time trajectory of log (R/P); **(c)** stock-recruitment scatterplot, in same units as (a).

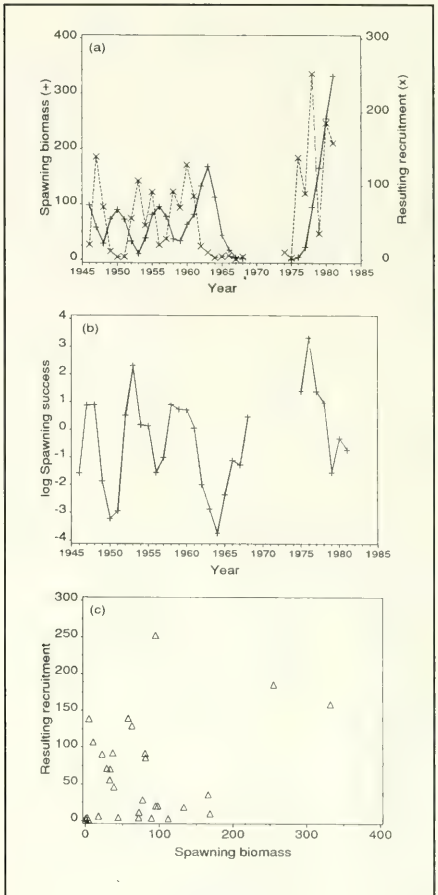

Figure 3

Recruitment of the chub mackerel *Scomber japonicus* stock off southern California. **(a)** Time trajectories of recruitment R (10^9 lb) and spawning biomass P (10^9 lb); **(b)** time trajectory of log (R/P); **(c)** stock-recruitment scatterplot, in same units as (a).

other pesticides. The sharp rise in pesticide use in the 1950s and the subsequent decline in the 1960s and 1970s are similar for many of these compounds, which leads to difficulty in distinguishing their effects statistically. The PCBs, a group of non-pesticide toxic organochlorine compounds, have been used increasingly throughout most of this century, but little is known about the volume of their use and discharge before 1960.

Loadings of metals have varied with growth of the human population and also with fluctuations in patterns of industrial use. Loadings of some particularly toxic metals, such as lead and cadmium, have declined recently because of environmental regulations.

Most of the historical reconstructions of Summers et al. (1988) included values for all years from 1946 through 1981, but some contaminant variables lacked values for 1981. We extrapolated from immediately-

Table 2

Data available on contaminant loadings and other human impacts to the coastal waters of southern California, used for modeling spawning success of three coastal pelagic fish species. Headings indicate major categories. Variables were also assigned to groups (in parentheses) for principal-components analyses, used to reduce the number of variables before modeling. Asterisks (*) indicate variable not used for modeling.

Type of data	Years available
Gross indicators (Indicators group)	
Human population	1890–1980[a]
Municipal wastewater flow*	1890–1985
Physical-biological factors (Indicators group)	
Kelp harvest	1916–1985
Dredging volume	1900–1983
Power-plant cooling flow	1928–1985
Nutrient loadings (Indicators group)	
Nitrogen	1910–1986
Phosphorus	1910–1986
Total organic carbon	1910–1986
Organochlorine loadings (Organochlorines group)	
Aldrin	1945–1982
BHC or Lindane	1945–1982
Chlordane	1945–1982
DDT	1945–1982
Dieldrin	1945–1982
Endrin	1945–1982
Heptachlor	1945–1982
Polychlorinated biphenyls	1929–1986
Toxaphene	1945–1982
Metal loadings (Metals group)	
Cadmium	1920–1980[b]
Chromium	1929–1980[a]
Copper	1929–1980[b]
Mercury	1929–1980[a]
Nickel*	1945–1980[c]
Lead	1929–1980[b]
Zinc	1929–1980[b]

[a] Value for 1981 extrapolated from 1979 and 1980 values.
[b] Value for 1981 set equal to 1980 value.
[c] Time-series contains missing values within this period.

preceding values as necessary (Table 2). The extrapolated 1981 values, although necessary for the principal-component analyses, had very little influence on later calculations.

The reconstructions of Summers et al. (1988) comprise the best available dataset, and the only one on this scale, describing contaminant loadings off southern California in recent decades. Because of this, verification is difficult. Prager & MacCall (1990) found that the reconstructions agreed fairly well with some recent estimates of metals loadings made by the Southern California Coastal Water Resources Project (SCCWRP), which has monitored fluxes of metals from southern California sewage outfalls since 1971 (Konrad 1989). However, only a small portion of total metals loadings are in sewage; this may have caused the discrepancies noted for some metals by Prager & MacCall (1990). We also compared reconstructions with a study of metals deposition in anaerobic sediments in the Santa Barbara basin (H. Schmidt & C. Reimers, Scripps Inst. Oceanogr., La Jolla CA, pers. commun.). However, the sedimentary record, much less precise than the reconstructions, was unable to discern any clear trends or patterns in metals since 1932.

Explanatory data: Climate

A large suite of climate data (Table 3) for the years 1920–84 was compiled by Prager & MacCall (1987a,b,c), who described the data sources and processing in detail. Most of the raw data were provided by Dr. Andrew Bakun (Pac. Fish. Environ. Group, NMFS Southwest Fish. Sci. Cent., Monterey CA).

We detrended most of the sea level (SL) and sea-surface temperature (SST) series to remove rising trends with time. Values for 1983 were not used in computing trend lines, to prevent this extreme El Niño year near the end of the series from distorting the results. Only the series of SST in San Diego did not exhibit a significant trend, and accordingly that series was not detrended.

Seasonal effects were removed by standardizing each variable to zero mean and unit standard deviation (SD) by month of year. For example, the January values (1920–84) of Los Angeles rainfall were standardized as a group to mean 0.0 and SD 1.0. Standardization was performed separately for each month and time-series.

The climate dataset had a few missing values that we replaced with estimates. We used the BMDP procedure AM (Dixon et al. 1983) to estimate these values by stepwise regression on the available data. Reasonableness of the estimates was verified by simulation and by comparison with the nonmissing data (Prager & MacCall 1990).

Principal-component analyses

Many of the explanatory variables contained redundant information. For example, sea-surface temperature and sea level exhibit very similar patterns over time, as both are related to El Niño conditions and the flow of the California Current. Another example, noted above, is that many contaminant time-series are tightly

Table 3

Summary of climate data used for modeling spawning success of three coastal pelagic fish stocks off southern California. Headings indicate major categories. Variables were also assigned to groups (in parentheses) for principal-component analyses used to reduce the number of variables before modeling.

Type of data and station location(s)	Years of monthly data available
Rainfall (Rainfall group)	1920–1984
San Francisco, Oakland	
Los Angeles, Long Beach	
San Diego	
Seawater salinity (Rainfall group)	1920–1984
Scripps Pier: surface	
Scripps Pier: bottom	
Sea-surface temperature (El Niño group)	1920–1984
Farralon Islands	
Pacific Grove	
San Luis Wharf	
San Diego	
Sea level (El Niño group)	1920–1984
San Francisco	
Los Angeles	
San Diego	
Bakun's upwelling index (Upwelling group)	1946–1984
30°N, 119°W	
33°N, 119°W	
36°N, 122°W	
39°N, 122°W	

coupled to human population size, which generates them. This multicollinearity causes problems in fitting and interpreting statistical models such as ours. In extreme cases of multicollinearity, numerical algorithms used for fitting can fail. A more likely problem is that interpretation is not straightforward, because parameter values depend upon the other variables in the model. When sea-surface temperature is included in a model, for example, it may explain a large amount of the variance associated with sea level, so there is little to be gained from including sea level itself in the model. Yet an effect may truly be due to sea level (or to the strength of the California Current), and this relationship may thus be overlooked. Because of this difficulty, any biostatistical study of this nature is inherently unable to isolate the effects of individual causes. An important related practical problem is that a large number of potential explanatory variables makes any fitting procedure unwieldy.

We addressed some of these statistical problems by combining the explanatory data into new composite variables that did not contain duplicate information. These new variables, constructed by principal-component analysis, are linear combinations of the original variables. To reduce the number of variables (initially ~216) to a number more easily analyzed by standard statistical software, data on sea level, sea-surface temperature, and salinity were converted to bimonthly means; also, surface and bottom salinities at Scripps Pier were averaged. Monthly rainfall values were transformed into an annual value of total rainfall (preceding 1 July to current 30 June) and a value representing the median date of the season's rainfall. The explanatory dataset with these changes contained 94 variables before reduction by principal-component analysis.

We constructed two separate sets of principal components. The first set was constructed from physical and climate data (Table 3) but not data on contaminants or general stressors (Table 2). A recruitment model based on this analysis would show how much of the variability in spawning success could be attributed to stock size and climatic variation alone. The second principal-component analysis included all explanatory variables, and was used to reveal how much more variability could be explained by adding contaminant information to the analysis.

Weighting was used in the principal-component analyses to avoid giving undue emphasis to variables (e.g., SST) measured at many locations. To determine weights, each variable was assigned to one of six groups, as shown in Tables 2 and 3. Each group received 1/6 of the total weighting, which was divided equally among the variables within the group.

The results of principal-component analyses are frequently difficult to interpret, as the components are formed on purely statistical grounds. Extensive graphical analysis (presented in Prager & MacCall 1987c, 1990) allowed attaching an interpretation to some, but not all, of the components used in these analyses (Table 4). In interpreting results of the recruitment models, we used a different approach, that of measuring the correlation of the model's explanatory effect with the individual variables, as explained below.

Application of model to three fish stocks

Overview

For each stock, we developed two alternative models: one using the principal components of climate data only, and the second using the principal components of climate and contaminant data. We then examined correlations of each model's estimated explanatory time-series (i.e., the summation on the right side of Eq. 3) to the original climate and contaminant variables. Be-

Table 4

Interpretation of principal components (PCs) used as explanatory variables in models of spawning success in three coastal pelagic fish stocks off southern California. Variables W_1–W_{10} are PCs of data on climate; variables C_1–C_{10} are PCs of data on climate and on contaminant (e.g., metals, organochlorines) loadings. Because interpretation of PCs is difficult, other methods were used to interpret model results (Fig. 4–6; text). SST = sea-surface temperature, SL = sea level.

Variable	Interpretation
W_1	Heavy rainfall; elevated SL and SST; W_1 has peaks in 1958 and 1983 corresponding to El Niño events.
W_2	Very low rainfall, high SST and SL in second half of year.
W_3	Increased upwelling, especially in mid-year.
W_4	Late rainy season with lower-than-average rainfall, decreased SST at northern stations.
W_5	Reduced upwelling at 30°N station, late rainy season.
W_6	Late rainy season in San Francisco.
W_7	Heavy rainfall in San Francisco, high early-year salinity in La Jolla.
W_8	No clear interpretation.
W_9	No clear interpretation.
W_{10}	No clear interpretation.
C_1	Increased upwelling midyear; high loadings of metals, nutrients, and most organochlorines; C_1 is in part a trend component, increasing from 1945 to 1978 and declining slightly thereafter;
C_2	High loadings of organochlorines, Cd, Cr, and Pb; reduced rainfall.
C_3	Elevated SL and SST, heavy rainfall; highest in years of El Niño events.
C_4	Elevated upwelling, especially at 30°N station; high loadings of Cr and BHC; C_4 is high around 1970, lower in other years.
C_5	Early, wet, rainy season, especially in San Francisco.
C_6	High loadings of Hg, early rainy season in southern California.
C_7	No clear interpretation.
C_8	No clear interpretation.
C_9	No clear interpretation.
C_{10}	No clear interpretation.

cause one of the models contained no contaminant data, agreement between the two models on the importance of contaminant variates was considered an indication of severe and troublesome collinearity between relevant climate and contaminant variables. Alternatively, it might simply indicate no contaminant effects. In the presence of strong contaminant effects, and lacking such severe collinearity, one would expect the explanatory effect from the model including contaminants to be more highly correlated with the contaminant variables.

Selection of explanatory variables

It is widely recognized by modelers and statisticians (e.g., Gilchrist 1984:11) that a profound source of uncertainty in statistical modeling is the possibility of error in specifying the model's structure. Such specification error biases parameter estimates and renders most confidence intervals and hypothesis tests invalid (Kennedy 1979, Gilchrist 1984). Unfortunately, the possibilities of specification error and its ramifications are often overlooked when statistical models are used in ecology. The models chosen and presented here were undoubtedly misspecified; they may have included unimportant effects or omitted important ones, and they were limited to a linear functional relationship, which is unlikely to be the true one.

After specifying the linear structure of Eq. 3, choice of variables was the main concern. When no theoretical basis exists to guide it, choice of variables in a regression model must be regarded as heuristic. Neither the theory of the underlying discipline—ecology—nor that of statistics can answer this question unequivocally, so we were forced to use an empirical approach. We started by retaining only the first 10 components from each of the principal-component analyses. (In each case, this retained ~80% of the weighted variance.) To arrive at a parsimonious model, we fit regression models to all combinations of 10 or fewer variables and ranked the many models by C_p, a goodness-of-fit statistic from Mallows (1973). For each combination of stock and data type (climate or combined), we accepted the model with the lowest C_p. However, alternative models of similar fit were similar in structure.

Any method of variable selection in which many candidate explanatory variables and combinations of variables are examined may lead the investigator to accept models which fit well solely through chance. This point has recently been emphasized by Flack & Chang (1987). Although the use of C_p is a relatively conservative approach, the true statistical significance of our results is unknown. Thus we view the modeling exercise as one of hypothesis generation, rather than hypothesis testing. The limitations of inference that come from an empirical choice of model structure are not unique to this study; they pertain to all modeling exercises except those in which

the final model structure and set of explanatory variables are correctly chosen before fitting. Here, we use elements of hypothesis testing, but acknowledge the impossibility of testing the hypotheses rigorously.

Detecting the influence of contaminants

We started with the following null hypothesis: "any apparent influence of contaminants can be explained by random variability alone, including chance correlations of contaminant loadings with climate variability." We imposed three statistical criteria to be met before we would consider rejecting this null hypothesis on the basis of a model including contaminant-loadings data. The first criterion was qualitative: the correlations of the model's explanatory effect with most contaminant variables had to be negative. The other criteria were quantitative: the regression coefficients of the model had to be statistically significant at α=0.05, and the inclusion of contaminant information had to provide more explanatory power than use of climate data alone. If all three criteria were met, we would admit the possibility of contaminant influence on spawning success. The three criteria are described in more detail immediately below.

Sign test Of the variables in Table 3, the metals and organochlorines have been found by bioassay to have deleterious effects on fish (Weis & Weis 1989). (We omitted nickel because of an incomplete time-series and, more importantly, its relatively low toxicity.) Power-plant cooling flow also is generally considered deleterious, but the remaining variables in the indicators group could be favorable as well as unfavorable. The signs of the correlations with the 16 "deleterious" variables were subjected to a (one-tailed) statistical test of the following null hypothesis: "The observed number of negative correlations could arise by chance alone." Under this null hypothesis, the probability of a negative correlation between a contaminant variable and the model's estimated explanatory time-series is 0.5. Assuming independence among the 16 contaminant variables (an assumption that may be violated; see below), the probability of obtaining x negative correlations by chance is given by the binomial probability f(x; n=16, p=0.5). The probability of observing 11 or more negative correlations is 0.105, and of observing ≥12 is 0.038. Thus, the conventional error rate of $\alpha \leq 0.05$ requires ≥12 negative correlations between the 16 deleterious contaminant variables and the explanatory time-series from a model that uses the combined explanatory data.

Such a test concludes that apparent contaminant effects are qualitatively significant if 12 or more negative correlations are found. However, the true probability of Type-I error is >0.038, because many of the contaminant variables are positively correlated with one another, violating the assumption of independence in the binomial probability model and increasing the tail probabilities. While we cannot calculate an exact critical value of x in view of lack of independence, the value would be larger than the nominal value of 12 required for a model to pass this test.

Test of coefficients This test was used to assess whether the coefficients of the chosen model were significantly different from zero. Although we always chose the model with lowest C_p, that criterion does not depend directly on how precisely the regression coefficients are estimated. To test the significance of regression coefficients, we used the standard t-tests (at α=0.05) provided by the statistical software, and required all coefficients to be significant for the model to pass the test.

Improvement-in-fit test Our third criterion required that the model that incorporated contaminant information (i.e., which used the combined explanatory data) had to provide a substantially better fit to the spawning success data than the model using the climate data alone. To judge this, we used the Schwarz criterion (Smith 1988), a statistic for comparing non-nested models. The Schwarz criterion requires an estimate of σ, the true model variance; we used the MSE of the better-fitting model. To pass the test, the model with combined data was required to have a higher value of this statistic than the model with climate data.

Results

Northern anchovy

Not unexpectedly for a short-lived species, the spawning biomass of this northern anchovy stock appears to depend strongly upon the preceding few years' recruitments. A peak in spawning biomass generally follows a corresponding peak in recruitment by 1 or 2yr (Fig. 1a). The stock-recruitment relationship, although noisy, appears density-dependent, in that spawning success improves at lower stock sizes (Fig. 1c), and each model includes a significant compensatory term (the negative stock-size parameter; Table 5). Ricker (1954) and MacCall (1980) have pointed out that cannibalism of eggs or larvae by the adults could cause such compensation.

Neither the climate model nor the combined model explained even half of the variability in log spawning success of northern anchovy (Table 5). Although the model incorporating contaminants had somewhat

Table 5

Summary results of regression models of logarithm of recruits per spawner for three coastal pelagic fish stocks off southern California. Predictor variables were parent stock size (P) and either principal components (W_i, i=1, ..., 10) of climate data (models denoted ○) or principal components (C_i, i=1, ..., 10) of climate data and data on contaminant loadings (models denoted ●). Each model also included an intercept. Variable selection used an all-subsets algorithm with the C_p statistic; thus models may include variables not significant at P<0.05, and all P values are considered nominal.

	Variables included in model (with sign of coefficient) and nominal probabilities of t-statistics for H_0: coefficient = 0.	df of model, error	F statistic	Nominal Prob > F	R^2
	Northern anchovy *Engraulis mordax*				
	$-P$, 0.025; $-W_6$, 0.13	2, 15	4.20	0.036	0.36
●	$-P$, 0.17; $-C_5$, 0.087; $-C_7$, 0.13	3, 14	4.14	0.027	0.47
	Pacific sardine *Sardinops sagax*				
	$-W_3$, 0.030	1, 15	5.77	0.030	0.28
●	$-P$, 0.0004; $-C_1$, 0.0001; $-C_3$, 0.002; $+C_{10}$, 0.002	4, 12	14.4	0.0002	0.47
	Chub mackerel *Scomber japonicus*				
	$-P$, 0.0001; $-W_2$, 0.015; $+W_4$, 0.021; $+W_6$, 0.008; $-W_7$, 0.023; $-W_{10}$, 0.09	6, 23	6.74	0.0003	0.64
●	$-P$, 0.0003; $+C_3$, 0.094; $-C_4$, 0.004	3, 26	8.11	0.0006	0.48

higher R^2 and nominal significance level* than the model including only climate effects, it is impossible to attribute this difference to the effects of contaminants on recruitment. Given the small sample size and relatively small difference in fit, it seems more logical to attribute it to chance.

The two models of anchovy spawning success can be compared by plotting the correlations of the two corresponding explanatory effects with the original explanatory variables (Fig. 4). For some variables (e.g., those related to rainfall), correlations are similar between models; however, many other variables fall into the second and fourth quadrants of the plane, meaning that they are positively associated with spawning success in one model and negatively associated in the other. For example, the two models assign opposite signs to the influence of most upwelling variables. Based on this inconsistent pattern of correlations (Fig. 4) and the lack of nominally significant parameters (except for the stock-size parameters) in Table 5, we conclude that these models identify neither climate- nor contaminant-related variability in the spawning success of this stock.

Indeed, the major determinants of anchovy recruitment strength remain to be discovered. Smith (1985) speculated that recruitment might be controlled in late-larval stages through "plasticity of the interaction between growth rate and survival." Peterman & Bradford (1987) detected a decrease in larval survival associated with episodes of high wind speed; however, Peterman et al. (1988) did not detect significant corre-

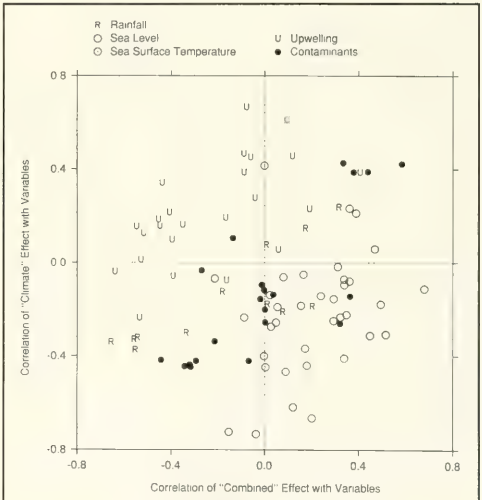

Figure 4

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of northern anchovy *Engraulis mordax* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Plot suggests that neither model offers a clear explanation of anchovy spawning success.

*To emphasize the impossibility of determining true significance levels, reported significance levels are denoted "nominal."

lation between abundance of larvae and of later early stages or between larval abundance and subsequent recruitment. Because our explanatory data do not include wind speed, we were unable to address this specific question. Cury & Roy (1989) demonstrated that spawning success in coastal pelagic fishes responds nonlinearly to upwelling, but our linearized model could not include this possible relationship.

Methot (1989) has shown that the age of maturity in northern anchovy increases from 1 to 2 when temperatures are below average. Our data already account for this effect, because the spawning-stock estimates of Methot (1989) incorporate this effect of temperature.

The only other likely determinant of anchovy recruitment is spawner abundance itself. This is a straightforward phenomenon in which very low abundance produces very low recruitment. Our stock-recruitment plot (Fig. 1c) does not illustrate this phenomenon; however, the plot begins after the lower abundances of the 1950s, when the effect would have been most pronounced.

Pacific sardine

As in the northern anchovy, the spawning biomass of Pacific sardine depends strongly upon immediately-preceding recruitments, with peaks in recruitment preceding peaks in spawning biomass by about 2 yr (Fig. 2a). Interpretation of the stock-recruitment plot (Fig. 2c) is problematic: If the 2 yr of highest spawning biomass (1949 and 1950) are disregarded, the plot appears biphasic, with small spawning biomasses producing small recruitments and large biomasses producing large recruitments. But if all years are included, recruitment appears to be density-dependent (or strongly influenced by external factors). The stock-size effect estimated by the model with climate effects was not significant (P=0.66); we refit the model without a stock-size effect (Table 5), reducing the R^2 by only 1%. The model with combined climate and contaminant effects identified a statistically significant stock-size effect with the correct sign for compensation (Table 5). This model also fit the data much better.

The two models give quite different pictures of the climatic effects associated with good spawning success in this Pacific sardine stock (Fig. 5). Correlations with rainfall-related signals were mostly negative for both models. Sea level and sea-surface temperatures were estimated to have mostly negative effects in the climate model, but many of these were estimated as positive in the combined model. Correlations with upwelling variables were all positive in the climate model, but were mixed in the combined model.

Most correlations with contaminant variables were negative in both models. In the climate model, correla-

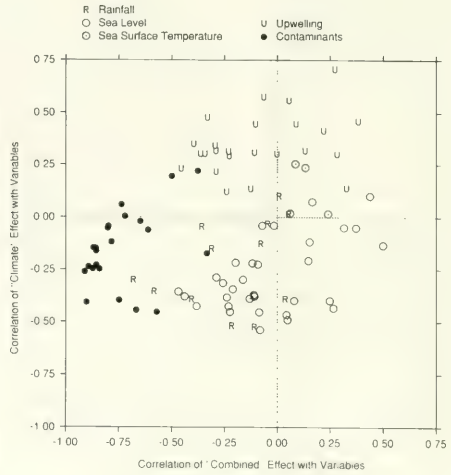

Figure 5

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of Pacific sardine *Sardinops sagax* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Stronger negative correlations of "combined" model suggest that contaminants have had a negative effect.

tions ranged from ~0.25 to –0.50. In the model with combined effects, the correlations ranged from ~ –0.25 to ~ –0.95. These strong and consistently negative correlations are consistent with the hypothesis that contaminants affected the dynamics of the Pacific sardine stock, perhaps contributing to its collapse.

Chub mackerel

The models of chub mackerel spawning success included statistically-significant, compensatory stock-size parameters of similar magnitude (Table 5). Compensation has been demonstrated in previous analyses of this stock (Parrish & MacCall 1978, MacCall et al. 1985), and is apparent in Fig. 3b.

Including contaminant variables added little to the model. The climate model had lower MSE than the combined model, and its nominal significance level was more extreme (Table 5). One is left with the impres-

sion that adding the contaminant variables merely muddied the picture.

The two models give similar pictures of the forces that appear to be associated with variability in spawning success of chub mackerel (Fig. 6). We consider the climate variables first. Both models showed moderate-to-strong positive correlations of spawning success with sea-surface temperature early in the year, moderate-to-positive correlations with sea level early in the year, and weak-to-moderate correlations with upwelling later in the year. Correlations with rainfall-related variables were weak.

The models were also similar in correlations with contaminant variables. Correlations with metal loadings were weak-to-moderate, but of different signs for different metals; this suggests chance (noncausal) correlations. Much of the signal in the metal loadings occurred in the late 1960s and beyond, when the chub mackerel stock was declining from overfishing and then recovering (MacCall et al. 1985); this coincidence could have induced noncausal statistical correlations. Correlations with organochlorines were negative. In interpreting this, it is relevant that spawning success in chub mackerel is highly autocorrelated and appears periodic (Fig. 3b). The organochlorine abundances are also very highly autocorrelated, usually consisting of a single peak. This could easily lead to correlations like those observed, even if the observed contaminant levels did not affect spawning success.

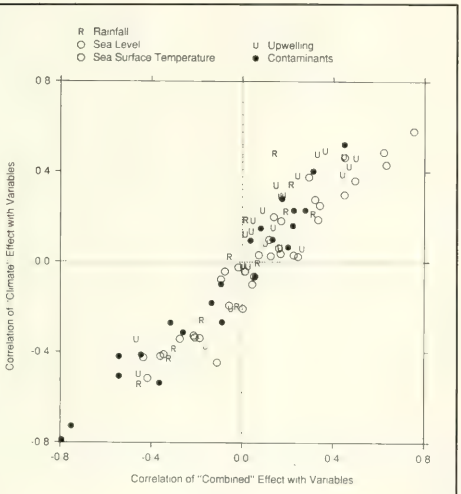

Figure 6

Comparison of two regression models of logarithm of spawning success (recruits/spawner) of chub mackerel *Scomber japonicus* stock off southern California. Models include effects of stock size and environment. Coordinates of a point are the correlations of the models' explanatory effects (see text) with an explanatory variable. For legibility, only category of variable (point) is indicated. Vertical axis: correlations with model estimated on climate data. Horizontal axis: correlations with model estimated on combined climate and contaminant data. Points in first and third quadrants of plane indicate agreement between models as to a variable's effect; points in other quadrants indicate disagreement. Strong agreement between models suggests that addition of contaminant data adds little to this model.

Although several contaminants correlate very highly with spawning success, the correlation patterns are nearly identical for the two models, one of which contains no information on contaminants. We interpret this to indicate that any contaminant effects are indistinguishable from effects of climate variables that fluctuate similarly over time. The strong agreement between the two models also suggests that recruitment-based contaminant analyses of this stock may be exceptionally prone to Type-II error, i.e., failure to detect any contaminant effects that might actually be present.

Parrish & MacCall (1978) also explored the effects of climate on chub mackerel spawning success, but comparison of this work and theirs is difficult for two reasons. Parrish & MacCall (1978) examined many explanatory variables not included in this study. In addition, changes in the estimated maturity schedule and the VPA-based stock and recruitment information (Prager & MacCall 1988) have resulted in a markedly different, as well as considerably extended, stock and recruitment series. Nonetheless, many of our estimated correlations agree with those of Parrish & MacCall (e.g., the positive effects of sea-surface temperature in the south, and the upwelling index at 30°N). Whereas Parrish & MacCall found that spawning success had a negative correlation to sea level at La Jolla, we estimated positive correlations with sea level at La Jolla and Los Angeles from January to June and independence in the later months.

Statistical evaluation of contaminant effects

In a preceding section we developed three statistical criteria for admission of possible contaminant effects. The sign test required 12 negative correlations between 16 "deleterious" contaminant variables and the explanatory effect of a model using the combined explanatory data. Correlations for models of all three stocks were mostly negative. Models of northern anchovy (Fig. 5) and chub mackerel (Fig. 6) each contained 11 negative correlations, but neither result was sufficient to reject

the null hypothesis. However, all 16 correlations were negative for the Pacific sardine (Table 6).

Regression coefficients were significant in models of Pacific sardine and chub mackerel. The model of northern anchovy spawning success fit relatively poorly (Table 5), and although the overall model was statistically significant, the individual regression coefficients were not.

According to the Schwarz criterion S, the models using combined data were marginally preferable to the models using climate data for chub mackerel and northern anchovy (S increased in the third significant figure). For sardine, the combined model was strongly preferable (S in ratio 2:1). Even allowing that the chub mackerel and northern anchovy models passed this test, the only stock to pass all three tests for suspicion of contaminant effects was the Pacific sardine.

Discussion

A somewhat similar biostatistical study was conducted by Martin Marietta Environmental Systems to examine possible effects of contaminants on fishes in five estuaries of the U.S. Atlantic coast, with emphasis on the Hudson-Raritan basin (Summers et al. 1985, 1987). The study used a categorical regression model of historical landings (Rose et al. 1986); the autoregressive model did not attempt biological or demographic realism. After accounting for the effects of hydrographic conditions and previous stock sizes, Summers et al. (1987) detected correlations related to contaminant variables including dissolved oxygen, dredging, and biochemical oxygen demand. The study concluded that there were consistent patterns of anthropogenic influences among similar stocks across different estuaries. In a second categorical regression study, Summers et al. (1990), while expressing some reservations about ultimate causes, concluded that sewage loadings have had a negative effect on white bass *Morone americana* production in the Choptank River, Maryland.

The present study was not undertaken with the expectation of finding clear evidence that contaminants affected fish stocks, nor clear evidence to the contrary. We knew of many reasons that contaminant effects might be difficult to detect, including major theoretical and practical difficulties in the data, shortcomings in biological knowledge, and the limitations of available statistical methodology (for details, see Appendix). As expected, we failed to detect contaminant effects on anchovy or chub mackerel, although we are unable to state whether this reflects a lack of such effects or merely low statistical power. In contrast, the results for Pacific sardine suggest that contaminant stress, at a time of severe overfishing, contributed to the decline and collapse of this stock. Partly because we searched for the best among many possible models, we cannot attach any level of statistical certainty to this suggestion. Our search selected a model of high explanatory power (R^2=83%) in which contaminants were strongly represented, and that, we believe, makes a strong case for further research into the question. Important areas of research would include investigating how such a model of historical events, not formulated a priori, can be statistically validated (or invalidated); which individual contaminants may have contributed to the stock collapse; and by what mechanisms contaminants may have played a role in the decline of Pacific sardine.

An alternative hypothesis about Pacific sardine is that the true spawning-success relationship is depensatory rather than linear, and thus depensation, rather than exogenous influences, mediated the decline of the stock. Consistent with this hypothesis, the stock-size component of our model (Fig. 7a) fits the observed spawning-success data quite well until the mid-1950s (years of very low population size) when the stock-size component predicts higher spawning success than was observed. To examine this alternative hypothesis in more detail, we fit spawning-success models using the following variant of the gamma function:

Table 6

Statistical criteria used to screen models of spawning success of three coastal pelagic fish stocks off southern California. As predictors, models used parent stock-size and principal components derived from measures of climate and of contaminant loadings. Models were required to meet all three criteria in this table before being considered suggestive of contaminant influences on spawning success.

Statistical criterion	Fish stock		
	Northern anchovy	Pacific sardine	Chub mackerel
Number of significant negative correlations with contaminants thought to be deleterious (12 required).	11	16	11
Significance of coefficients in model that included contaminants.	no	yes	yes
Improved fit of model including contaminants, compared with model including only climate. (Improvement judged by Schwarz criterion.)	yes	yes	yes

$$\log(R/P) = \alpha + \gamma \ln P + bP + \sum_{i=1}^{m} \theta_i x_i + \varepsilon. \quad (4)$$

This differs from our original model, Eq. 3, only in including the term containing the estimated parameter γ. When $\gamma = 0$, this term drops out and the model is equivalent to Eq. 3. When $\gamma < 0$, the model is more strongly compensatory than Eq. 3; when $\gamma > 0$, the model is depensatory. In results of fitting this model, the depensatory effect was estimated as significant only in the absence of climate or combined variables ($\hat{\gamma}$= 1.57, $P < 0.025$ for a one-sided t-test). With the introduction of climate variables, the depensatory effect became smaller and not statistically significant ($\hat{\gamma}$=1.02, $P < 0.19$); with the introduction of the combined variables, the depensatory effect disappeared ($\hat{\gamma}$= –0.53, the wrong sign for depensation). In the model with a depensatory parameter, correlations of the explanatory effect (summation term in Eq. 4) with contaminants were within 2% of those obtained from the model without the depensatory parameter. Of course, the correct specification of spawning-success relationships may be more complex than even Eq. 4. Nonetheless, these results indicate that a simple model including depensation cannot account for the observed decline in spawning success residual to stock-size effects. When this decline, as modeled by our combined variables (Fig. 7b), is combined with Ricker stock-size effects, the resulting model fits well the observed data on Pacific sardine (Fig. 7c).

Are there plausible mechanisms by which contaminants may have contributed to the decline of the sardine population? The high fat content of sardines, anchovy, and mackerel makes them likely to accumulate fat-soluble compounds such as the organochlorines listed in Table 2. It is known that DDT has caused widespread reproductive failures in birds, including those in this geographical area (Anderson et al. 1975). Also, fish have been observed to depurate PCBs by transferring them into eggs (Binder et al. 1984). Since the early stages of many fish species have exhibited reduced survival rates after exposure to toxic compounds (Weis & Weis 1989), plausible mechanisms do exist. The Pacific sardine stock was under severe overfishing pressure at the time of its collapse, and such pressure would increase its susceptibility to environmental stress. The possibility that contaminants may be implicated in the collapse of a major marine fishery is a novel and startling one.

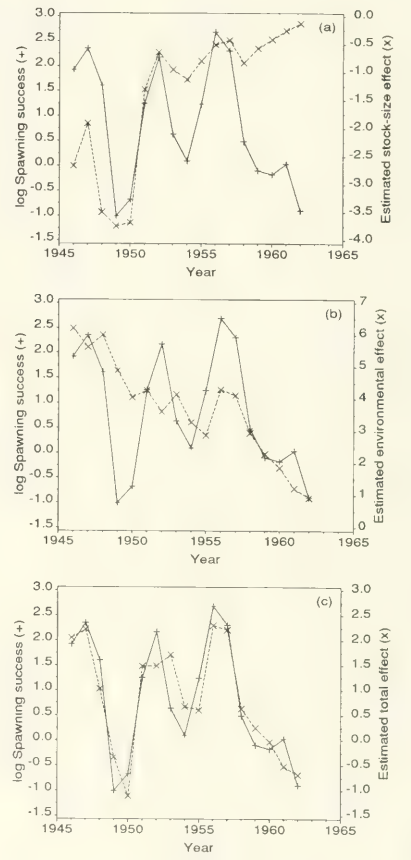

Figure 7

Components (dashed lines) of a model of spawning success (recruits/spawner) of Pacific sardine *Sardinops sagax* stock off southern California. Each panel also shows the observed spawning-success data (solid line) after logarithmic transform. **(a)** Model component associated with estimated stock-size (depensatory) parameter; **(b)** model component associated with estimated parameters corresponding to climate variability and contaminant loadings; **(c)** predicted values from full model (intercept plus stock-size and environmental effects). The environmental component is more influential in the mid-1950s and later, when contaminant loadings generally increased.

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Appendix

We encountered many statistical difficulties and uncertainties in our biostatistical approach to detecting contaminant influences. Anyone attempting to interpret our results or to conduct a similar analysis should be cognizant of the following issues concerning data, biological understanding, and statistical methodology.

Difficulties relating to the data

- imprecision in data on stock and recruitment;
- imprecision in measurements of physical (climatic) conditions;
- imprecision in measurements and reconstructions of contaminant loadings;
- lack of residence-time models for contaminants in the water column and sediments, necessitating the use of loading (influx) values, rather than estimated *in situ* concentrations;
- substantial environmental variability that cannot be modeled effectively, and that would thus become "noise";
- strong trends in some resource and contaminant histories that can produce ambiguous correlations between these quantities;
- time-series that are short by statistical standards, although long by comparison with others available;
- multicollinearity: similar patterns over time in different explanatory variables.

Shortcomings in biological understanding

- only rudimentary knowledge of biological response to environmental variability and contaminants;
- poor models of environmental influences on larval production and recruitment;
- poor knowledge of spawning-at-age schedules, especially in light of increased evidence of multiple spawnings within seasons;
- little knowledge of natural mortality rates for most species;
- little or no knowledge of the true form of stock-recruitment relationships for most species.

Problems with statistical methodology

- lack of methods to address the problem of errors-in-variables, except in the simplest cases;
- lack of methods to determine the statistical power of hypothesis tests; and
- lack of methods to identify conclusively a model with the optimum number of parameters, or, for that matter, the correct non-zero parameters;
- possible presence of nonlinear effects, but insufficient data to identify and estimate a nonlinear model.

Similar problems arise in diverse areas of biostatistical analysis of populations and ecosystems, including most studies conducted for fishery management.

We attempted to reduce the effects of collinearity among the explanatory variables by using principal-components analysis. Unfortunately, stock size was at times correlated to other variables. The inability to identify effects of individual climate or contaminant variates is an unavoidable result of collinearity. This problem was accentuated by autocorrelation in the explanatory data and in the stock and recruitment series. Time trends in several explanatory variables, including stock size, compounded the problem of multi-collinearity, as they can lead to spurious (noncausal) correlations.

Even after the principal-component analysis, the suite of possible explanatory variables was large. For parsimony, we chose subset models for each stock. As stated, it is nonetheless probable that our models contain specification error. There are three main forms of specification error: (1) omission of relevant variables or inclusion of irrelevant ones, (2) a wrong functional form for the model (e.g., quadratic response when linear is specified), and (3) changes in the true parameters over time. Consequences of specification error can include biased parameter estimates and biased estimates of variance (Kennedy 1979), which in turn can lead to reduced statistical power. Using principal components, which are biologically arbitrary combinations of variables, may conceivably contribute to specification error (including errors in variables, as defined below).

Most of the recruitment time-series derived from VPA were short and did not coincide exactly with the contaminant data series, themselves not exceptionally long. A major consequence of modeling with a small sample size is low statistical power.

Observation error in explanatory variables causes difficulties in OLS parameter estimates, including inconsistency and, in the bivariate linear case, bias towards zero (Theil 1971, Kennedy 1979). This is known in the field of econometrics as the "errors-in-variables" or "errors-in-predictors" problem, and is sometimes considered a special case of specification error (e.g., Theil 1971). It has been demonstrated that recruitment models used in fisheries are subject to this problem (Walters & Ludwig 1981, Goodyear & Christensen 1984). If one is interested only in a predictive model, the bias is not important. If the parameter estimates are the object, however—as in the present case—the bias is especially problematic because its direction and magnitude are

known only in a few simple cases. By analogy to the results in bivariate linear regression, we suspect that coefficients of our regression models are biased towards zero. The estimated correlations with individual explanatory variates, including contaminants, may also be biased towards zero because of the smearing of the relationship by errors in the predictors.

Further complication is caused by the strong correlations between potential explanatory variables reflecting climate and those reflecting contaminant loadings (Prager & MacCall 1990, Table 6.1). A few examples are the correlations between annual dredging removals and total rainfall in San Diego (r=–0.32), PCBs loadings and July–August SST at San Luis Wharf (r=0.63), and lead loadings and May–June upwelling at 39°N, 122°W (r=0.79). This collinearity makes it nearly impossible to distinguish, by statistical means, the effects of climate from those of contaminants.

Length-based analyses of yield and spawning biomass per recruit for black sea bass *Centropristis striata*, a protogynous hermaphrodite

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Abstract.—Dynamic pool models were originally developed to evaluate the effect of exploitation on gonochoristic species of fishes. Consequently, application of these models to hermaphroditic species may lead to erroneous conclusions. The objective of our analysis was to develop an alternative method for estimation of yield-per-recruit and spawning stock biomass-per-recruit that incorporates the effect of sex transformation. Life-history characteristics such as the rate of sex change, growth, and mortality are size-specific; therefore, a length-based model was produced using a series of time-invariant distributed delays. The model incorporates a sequence of length-stages through which the cohort moves, at rates determined from empirical length data. At each length-interval, fish may die, move to the next interval, or switch sex according to a probability distribution of transformation. The model tracks the cohort through time and length categories as an aggregation of individuals rather than a representative average. The estimate of yield-per-recruit for a protogynous hermaphrodite, black sea bass *Centropristis striata*, differed little from traditional models. The distributed delay model with a sex-transformation phase produced considerably lower estimates of spawning stock biomass-per-recruit than the model with traditional assumptions. Potentially erroneous estimates of biological reference points using standard methods for hermaphroditic species may be overcome with use of a distributed delay model, which can incorporate size-specific life-history dynamics.

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Analytical models describing the potential yield of a fisheries resource consist of three basic dynamic elements: population growth, recruitment, and mortality (Russell 1931). Dynamic pool models (e.g., Thompson & Bell 1934, Ricker 1954, Beverton & Holt 1957) are traditionally used to evaluate potential yield-per-recruit (Y/R) and spawning stock biomass-per-recruit (SSB/R) relative to fishing mortality and size-at-recruitment. Potential yield and spawning biomass of a cohort are typically calculated as a summation across discrete age-increments, under specified conditions of growth and natural mortality. Within each age-interval, growth and fishing mortality rates are assumed to apply uniformly to all members of the cohort (Gulland 1977). Not all individuals follow the same growth trajectory, however, and the susceptibility of individual fish to mortality is often a size—rather than age-dependent phenomena (Kirkpatrick 1984). Consequently, length-based models can provide a more precise and accurate depiction of cohort dynamics, in addition to using directly measurable variables that are often linked to management measures.

Traditional age-based models of Y/R and SSB/R may be particularly inappropriate for species with unusual and/or complex life histories. This may be true for hermaphroditic species that have unique reproductive stages that change as a function of fish size. For example, significant growth and mortality changes that occur following sexual transformation would not be accounted for in conventional Y/R models.

Hermaphroditism will also influence estimation of sex-specific mortalities. For example, as transformations occur in a protogynous hermaphrodite, females are lost from the cohort, creating the same effect as increased female mortality. The transformations increase the number of males in the cohort, reducing the apparent mortality of males. Consequently, the mortality estimates for each sex are not independent, and a potential bias may exist in estimating Y/R and SSB/R when sex-specific characteristics are not considered.

Black sea bass *Centropristis striata* is a protogynous hermaphrodite common along the continental shelf of the northwest Atlantic between Massachusetts and Florida. Growth in black sea bass is sexually dimorphic, with faster growth but lower maximum age in females (Lavenda 1949, Mercer 1978, Alexander 1981). Females commonly reach sizes of 38 cm and age 8 yr (Lavenda 1949); however, at sizes of 8–35 cm females may transform into males and enter the male growth regime. Males may grow

to 60 cm and age 20 yr (Lavenda 1949) with greater variability in size-at-age than females. Consequently, a black sea bass has three possible growth rates: female, male, and transitional. These differences in growth rates and variability in size-at-age between the sexes will influence the potential yield from a cohort.

An alternative approach for modeling changes in a cohort over time is use of delay models. Delay models were first developed in the field of industrial dynamics as a technique to monitor movement of individuals through a system of substages (Forrester 1961), and have since been modified to incorporate effects of attrition (mortality) and variability in timing of movements (Manetsch 1976, Vansickle 1977). The subclass of distributed delay models can be a useful tool to describe the movement of any item through a process or, in a biological context, through developmental stages (Manetsch 1976). Extending the model to include a series of consecutive processes, it has been used to simulate growth dynamics in marine crustaceans (Idoine & Finn 1984), insects (Ravlin et al. 1978, Schaub & Baumgartner 1989), and agricultural crops (Gutierrez et al. 1984, 1988). The major advantage of this model type is its focus on the aggregated behavior of individuals rather than a representative mean.

To estimate Y/R and SSB/R in black sea bass, we modeled the growth and mortality of a cohort as a series of distributed delays with an associated mortality, using length categories as individual developmental stages. This approach allowed us to simulate the decline of the cohort while retaining information about variation in size composition and size-specific mortality in the cohort. In addition, we were able to evaluate the influence of additional mortality on the population dynamics of a species with an hermaphroditic life history.

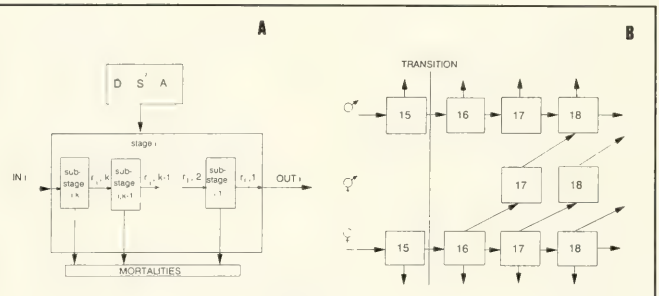

Figure 1

(A) Schematic of intra-stage flow of the distributed delay model: D = delay period defined as mean number of days necessary to move through a stage; S^2 = variance of D; A = instantaneous mortality rate; i = index of stage; INi = number of individuals entering stage i; k = integer value of $D^2/(S^2)$, which defines the number of substages within a stage; r_i = flowrate between substages; OUTi = number of individuals moving into next stage; mortalities = number of individuals removed from stage i through attrition. **(B)** Schematic of flow between cm stages in the model.

Methods

The model structure

Time-invariant distributed delay models with a mortality term (Vansickle 1977) can be characterized as a sequence of stages, with flow through each stage i represented by a series of differential equations (Fig. 1):

$$dr_{i,1}/dt = k/D[(x(t)-r_{i,1}(t))-(A(t)*D/k)]$$
$$dr_{i,2}/dt = k/D[(r_{i,1}(t)-r_{i,2}(t))-(A(t)*D/k)]$$
$$\vdots$$
$$dr_{i,k}/dt = k/D[(r_{i,k-1}(t)-r_{i,k}(t))-(A(t)*D/k)]$$

where $x(t)$ = input rate at time t,
k = integer value of D^2/variance of D (S^2) which defines the number of substages within a stage,
i = index of stage,
j = index of substage from 1 to k, and
$r_{i,j}$ = flowrate between substages j and j-1, stage i;

or
$$r_{i,j} = (k_i / D_i) * Q_{ij}$$

where Q_{ij} = the number of individuals in substage j, stage i,
D = delay period defined as the mean number of days necessary to move through a stage (the value of D at stage i varies by sex), and
$A(t)$ = mortality rate at time t.

All rates in the model are instantaneous. The model was simulated as a series of difference equations with a time step equal to 1 day. The delay model can be expressed either in terms of flows (r_{ij}) or state variables (Q_{ij}) (Vansickle 1977). For simulation purposes, this model utilizes flows within, between, and out of stages representing 1 cm length categories through which a cohort will pass. These flows were converted

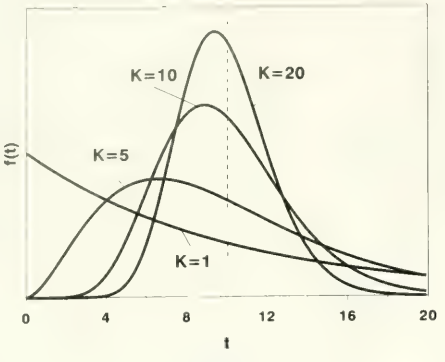

Figure 2
Erlang probability density function for various values of k and a mean t = 10.

to state variables (e.g., numbers of individuals dead due to fishing mortality at a given size) where necessary for analyses. Individuals in the cohort passed through each stage at a rate determined by an Erlang probability density function. The shape, or the order, of the density function was determined by the value of k (Manetsch 1976) (Fig. 2). Transit time of an individual through stage i was a function of the mean delay period (D) and associated variance. The greater the variance relative to the mean, the greater the value of k. This continuous function was approximated, using difference equations, by a series of substages. The number of substages within a stage was equal to the integer value of k, since fractional substages cannot be used in the discrete approximation necessary for the model.

A cohort entered length stage i at time t and moved through the substages at stage-specific rates. At time t+1, fish either moved into length stage i+1, remained in length stage i (at some substage), or were removed from the system at a defined rate of mortality due to fishing and/or natural mortality. At time t+2, some fish were still in stage i, some in i+1, and possibly some in i+2, etc. The biomass of the cohort and mean size changed as the distribution moved through the series of length stages until all individuals reached a maximum size or the cohort was eliminated through mortality. Any individuals moving to a size beyond the maximum were assumed to undergo senescence and were removed from the system at that maximum size. Yield was calculated from the number of individuals removed at each length stage ≥ the size of recruitment to the fishery × the ratio of fishing mortality/total mortality (F/Z). The biomass of fish removed via fishing mortality was calculated using the appropriate sex-specific length-weight equations. Spawning stock was calculated as the sum of the number of females per length remaining in the system at the time of spawning (1 June) × the probability of female maturity-at-length. The number of mature females-at-length was converted to biomass using a length-weight equation.

With this model, hermaphroditism was included by splitting the cohort into three growth regimes and using a size-specific probability of sex transformation. At the initial stage, the cohort was divided into an appropriate number of males and females, then passed through length stages at sex-specific rates. At a designated length-interval, females began transformation by passing through an intermediate transitional stage prior to entering the male growth sequence (Fig. 1).

Input parameters

Input parameters required in the model were mean transit time (D) and its associated variance (S^2) per 1 cm length-category in days and $days^2$, respectively, by sex; maximum potential length for each sex in the population; probability of sex transformation-at-length for females; a range of lengths-at-recruitment (L_c) to the fishery; instantaneous natural mortality rate (specific to length groups and sex if appropriate); a range of instantaneous fishing mortality rates; and the percentage of females mature-at-length. In addition, length-weight equations by sex were necessary for conversion of numbers-at-length to biomass.

Estimates of mean transit times and their associated variances for black sea bass were determined from back-calculation of scale data. Sea bass scales were collected in coastal Long Island during 1979–80, aged, and length-at-age back-calculated (Mark Alexander, Conn. Dep. Environ. Prot., Old Lyme, CT, pers. commun.). Daily time-increments of growth were chosen to provide estimates of k. Transit time (D) by cm-intervals was calculated as

$$D = 365 / \frac{[(S_n - S_{n-1}) * SL]}{S}$$

where S_n = scale annulus n,
S_{n-1} = scale annulus n-1,
S = total scale size,
SL = standard length of fish,

with the assumption of linear growth between annuli (i.e., D equal between cm-intervals $(S_{n-1}/S)*SL$ and $(S_n/S)*SL$). Thus, each individual scale provided estimates of transit times (D) by cm, up to the maximum length of the fish (SL). The means of D and S^2 were

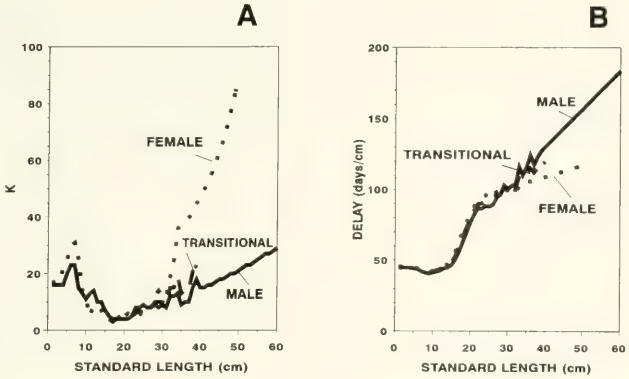

Figure 3

(A) Calculated values of number of substages, k, and **(B)** mean transit times, D, for female, male, and transitional stages of black sea bass *Centropristis striata*.

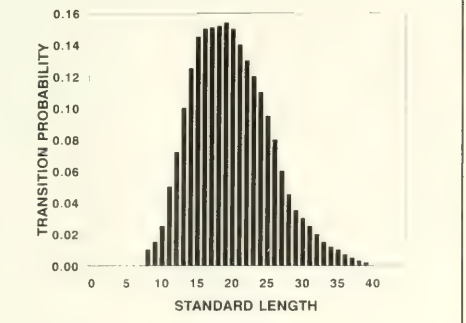

Figure 4

Transformation rates-at-length of female black sea bass *Centropristis striata* used in the delay model.

estimated per length category for each sex, with sex determined at the time of capture. Delay and variance estimates were extrapolated with a linear regression between the largest length categories in the dataset and maximum potential length (Fig. 3). Maximum lengths were 49 cm SL for females, 39 cm SL for transitionals, and 60 cm SL for males. D and S^2 for each length-interval in the transitional category were estimated by using the mean values of females and males. Transformation rates-at-length were estimated from a composite of the frequency of transitional-stage fish recorded in field observations (Fig. 4) (Mercer 1978, Low 1981, Wenner et al. 1986). Transformations began at 8 cm, and individual fish were allowed to exist in a transitional state for 1 cm. Sex-specific length-weight equations (Mercer 1978) used to convert standard length (cm) to weight in grams were

males: $wt=0.01773\ SL^{3.1525}$
females: $wt=0.02810\ SL^{3.0104}$
transitional: $wt=0.02120\ SL^{3.0991}$

Annual instantaneous natural mortality (M) for both the Y/R and SSB/R calculations was modeled as a length-dependent rate equal to 0.3 at lengths 1–10 cm and 0.2 at 11 cm–max. length. Instantaneous fishing mortality (F) was varied between 0.0 and 1.50 in both calculations. Mortality rates were applied over time-intervals of 1d (t=1/365).

Length-at-first-capture (L_c), which was modeled as knife-edge recruitment, varied between 16 and 32 cm SL. Increments were equivalent to annual mean lengths at successive ages, as determined from the delay model. The effect of harvesting was examined by incorporating an additional mortality term at each length category beyond the size-at-recruitment. Maturity-at-length data were collected during NEFSC bottom-trawl surveys between 1982 and 1990 (O'Brien et al. 1993). The initial cohort in the model consisted of 2000 fish divided according to a sex ratio of 99:1 female to male (Mercer 1978, Wenner et al. 1986). Precision of rounded values in the computer program resulted in the net loss of some individuals; therefore, the number of recruits used in the per-recruit calculations was the sum of individuals accounted for at the end of the run rather than the initial input value. The yield model was run for 25 yr or until the number of remaining fish in the cohort was <1; and the spawning biomass model (females only) was run for 11 yr or until the cohort was reduced to <1 fish. The Y/R and SSB/R models were developed as separate computer programs written in ANSI standard FORTRAN.

The Y/R estimates from the distributed delay model were compared with results from a Thompson-Bell (T-B) Y/R model. Lengths-at-annual-intervals for males and females were derived from execution of the delay model without a transitional phase and converted to grams using the appropriate length-weight equations. The mean of the male and female weights-at-age served as input to the T-B Y/R model. M was set equal to 0.3 for age 1, and 0.2 thereafter. The traditional SSB/R

model is a simple extension of the T-B Y/R model (Gabriel et al. 1989) and, consequently, the relationship to the delay models was similar. To avoid redundancy, only the relationship between the T-B Y/R model and the delay models was represented.

The sensitivity of the delay model to changes in the transition rates was examined. The transitional size-range was divided into 8 cm length-intervals and the transition rates within each interval were doubled. Spawning stock biomass-per-recruit was estimated for each interval of increased transition rates over a range of fishing mortalities and a constant size-at-first-capture of 16 cm.

Table 1

Mean length-at-age (cm) and variance from distributed delay model and mean back-calculated lengths-at-age (Mercer 1978) for black sea bass *Centropristis striata*.

Age (yr)	Distributed delay				Back-calculated	
	Male		Female		Male	Female
1	9.6	(0.56)	9.5	(0.45)	8.7	9.0
2	17.7	(0.89)	17.2	(0.96)	16.5	16.3
3	22.5	(1.25)	21.7	(1.20)	21.1	20.4
4	26.5	(1.65)	25.4	(1.64)	24.4	23.6
5	30.1	(1.85)	29.0	(2.20)	27.6	26.1
6	33.5	(1.92)	32.8	(2.35)	31.4	27.9
7	36.6	(1.93)	36.4	(2.17)	34.6	33.6
8	39.5	(1.91)	39.9	(2.11)	36.5	
9	42.3	(1.86)	43.2	(2.02)	38.4	
10	44.9	(1.82)	46.5	(1.84)		
11	47.4	(1.79)	48.4	(0.65)		
12	49.8	(1.76)				
13	52.1	(1.72)				
14	54.3	(1.68)				
15	56.4	(1.64)				
16	58.4	(1.31)				
17	59.5	(0.54)				
18	59.8	(0.18)				

Results

To confirm that the model accurately represented growth in the absence of any harvest mortality, we calculated the mean lengths of the cohort (by sex) at successive 365d periods as generated by the model, and compared the results with independent back-calculated mean lengths-at-age (Mercer 1978) (Table 1). Growth simulated by the delay model was comparable to growth observed from back-calculations, although sizes-at-age tended to diverge in older ages, with slightly higher lengths-at-age produced by the delay model. Under the influence of natural mortality only, a cohort introduced into the delay model was reduced to 0.1% of its initial number by the time the maximum length was attained. The reduction of the cohort using only natural mortality indicated that the model provided an accurate portrayal of the black sea bass growth rate for the stated set of mortality parameters.

To evaluate the effect of harvest mortality in the absence of sex transformation, we calculated Y/R as generated by the delay model without transition and compared the results with those obtained using the T-B model. Under various L_c values, yields-per-recruit from the two models were similar, indicating the basic

Table 2

Estimates of F_{max} for black sea bass *Centropristis striata* from distributed delay model with and without transitional phase and using Thompson-Bell model. Age-at-entry in yr.

Size (age) at entry	Distributed delay		Thompson-Bell
	w/ transition	w/o transition	
16 cm (2)	0.16	0.17	0.17
21 cm (3)	0.20	0.21	0.21
25 cm (4)	0.25	0.27	0.26
28 cm (5)	0.31	0.33	0.33
32 cm (6)	0.45	0.47	0.45
35 cm (7)	0.63	0.64	0.63

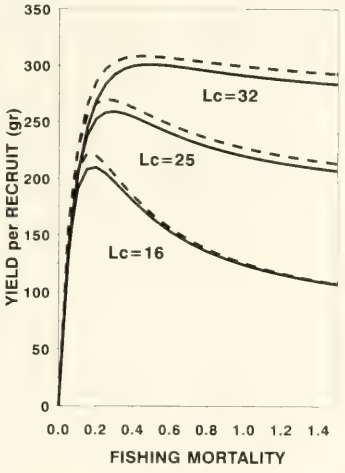

Figure 5

Yield-per-recruit for black sea bass *Centropristis striata* calculated by the distributed delay model without transitions (solid) and with a transitional phase (dash) at various alternative lengths-at-first-capture (L_c). M = 0.3 (1–10cm) and 0.2 (11–max. length).

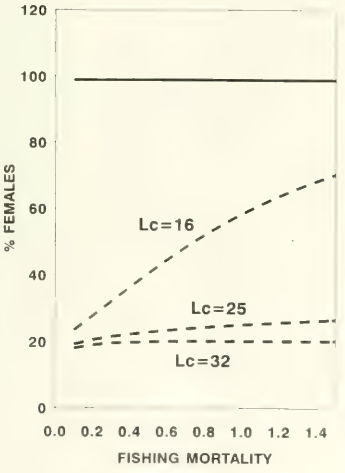

Figure 6

Sex composition of total yield for black sea bass *Centropristis striata* estimated from a distributed delay model with sexual transition (dashed) and without a transitional phase (solid) for varying sizes-at-first-capture (L_c).

delay model was comparable to traditional methods of estimating yield-per-recruit. The calculated biological reference point of F_{max} from both models was nearly identical (Table 2).

The addition of the transitional phase into the model had little effect on the estimates of Y/R. The calculated values of Y/R and F_{max} were similar for each recruitment size and fishing mortality (Fig. 5, Table 2). Although the effect of including the transition phase on the total yield was negligible, the effect on sex composition of that total yield was substantial. With no transition phase, the proportion of females in the yield was dependent upon the initial sex ratio, in this case 99% female (Fig. 6). If the sexual transformation of females to males was included, the percentage of females to the total yield increased as a function of F and decreased as a function of size-at-first-capture (Fig. 6). At a recruitment size of 16 cm SL (age 2), the percentage of female biomass in the yield went from 21.3% at an F=0.05 to 70.4% at F=1.5, whereas a change in recruitment size to 32cm (age 6) decreased the effect of F, resulting in a percentage range of 17.3–20.3% females for F=0.05 and 1.5 respectively.

The addition of a transitional phase had a significant impact on the estimates of SSB/R from the distributed delay model and subsequent estimates of a total female spawning biomass. In the absence of any harvest mortality, maximum SSB/R for a cohort that undergoes a transition was 600.8 g/recruit as compared with 2373.3 g/recruit without transition (Fig. 7). Over the life of the cohort, the spawning biomass-at-age increases similarly for the first 2 yr regardless of the form of the delay model (Fig. 8 for size-at-recruitment of 25 cm), at which point the effect of transition begins. At age 2.5, a cohort undergoing transition approaches the maximum contribution to spawning biomass-at-age, while a cohort that does not undergo transition makes its maximum contribution at age 10.

The inclusion of the transitional term in the model led to lower proportional reductions in SSB/R with increasing F. In a model without the transitional form (e.g., size-at-first-capture of 25 cm [age 4] Fig. 9) at fishing mortality of 1.5, the spawning potential was reduced to 15.2% of maximum spawning potential (%MSP). In a model with the transition term, however, 28.7% of maximum spawning potential was obtained (Fig. 9). The pattern is also obtained at other sizes-at-recruitment. The transitional phase also reduced the sensitivity of SSB/R to changes in F and size-at-recruitment (L_c). Decreasing F from 0.6 to 0.2 (L_c=25) increased SSB/R by 107% in the non-transitional model, but only 60.5% in the delay model with transitions. Similarly, an increase in size-at-first-recruitment from 16 to 32 cm (with F=0.6) increased SSB/R by 201.8% in the transitional model but 368.9% in the non-transitional version. The inclusion of a transitional phase increased the natural reduction in the number of females in the system, which consequently reduced the maximum SSB/R for the cohort and the relative influence of fishing mortality on SSB/R.

The sensitivity of estimates of SSB/R to changes in transformation rates was examined. Doubling the transition rate across all lengths decreased the SSB/R by 71% from 600.8 to 174.6 g/recruit. When the transition rates were doubled over 8 cm length-increments, the impact in SSB/R varied by F and the size-range over which the transformation rate was changed (Fig. 10). Doubling the rate of

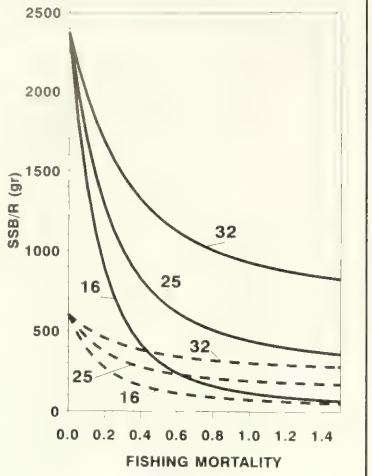

Figure 7

SSB/R for black sea bass *Centropristis striata* estimated from the distributed delay model without transition (solid) and with the transitional phase (dashed). M = 0.3 (1–10 cm) and 0.2 (11–max. length) with varying lengths-at-first-capture (L_c).

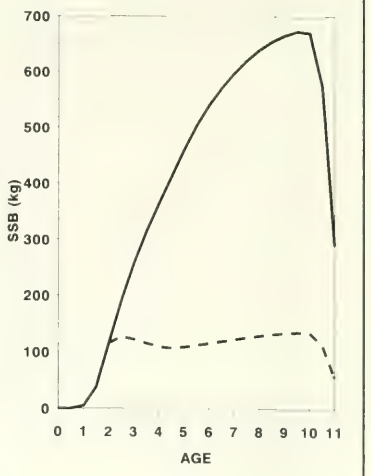

Figure 8

Spawning stock biomass-at-age for black sea bass *Centropristis striata* estimated with a distributed delay model with transitions (dashed) and without transitions (solid) for length-at-recruitment of 25 cm. M = 0.3 (1–10 cm) and 0.2 (11–max. length).

transformation in the 16–23 cm range had the greatest effect, decreasing SSB/R by 39.1% with F=0 (Table 3). Changes in transformation rates in the tails of the transformation probability distribution had little impact. In all cases, increases in F decreased the relative impact of transformation loss and, consequently, the sensitivity to changes in transformation rates decreased.

Discussion

Ignoring the unique population dynamics that may occur in hemaphroditic fishes will increase the risk of incorrectly estimating optimal exploitation levels from yield-per-recruit models (Bannerot et al. 1987). The problems can be compounded by disregarding the increased size variability within the system resulting from sexual transformations. Distributed delay models provide a mechanism for handling length-specific life-history changes, and results can be summarized as an aggregate of individuals and the associated variability rather than a simple mean estimate without error. The consequence is greater flexibility in dealing with changes between length categories without ignoring the size variability inherent within the system.

In the black sea bass example presented, the incorporation of a transitional term in the delay model had little effect on the estimate of yield-per-recruit. Since the sexes were combined to produce total yield, the growth differences between sexes were not large enough to produce significant changes in overall yield. Also, the inclusion of fishing mortality quickly removed any added yield contributed by transformed females. It is likely that the result would diverge further from a traditional model estimate as the differences in longevity or growth rate between the sexes increased.

The effect of modeling length- and sex-specific characteristics with a delay model was more apparent in spawning stock biomass-per-recruit estimates. The removal of female biomass via transformations was similar to increasing natural mortality at each length step, and consequently the spawning potential was reduced more quickly than under typical effects of fishing mortality and a constant M of 0.2. The system was more sensitive to changes in size-at-recruitment to the fishery than reduction in F at a constant size-at-recruitment.

The differences in spawning biomass-per-recruit estimates resulting from the distributed delay model have important management implications. If management

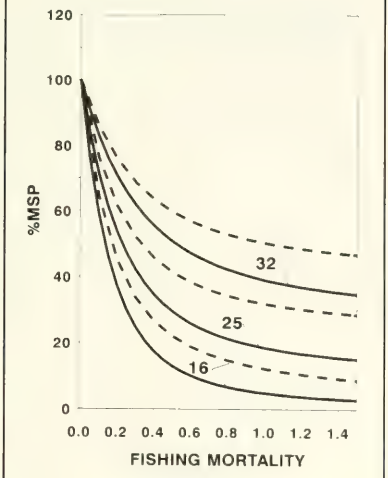

Figure 9

Percentage of maximum potential spawning biomass-per-recruit for black sea bass *Centropristis striata* under various fishing mortalities and lengths-at-first-capture (L_c) using the distributed delay model with transitions (dashed) and without transitions (solid).

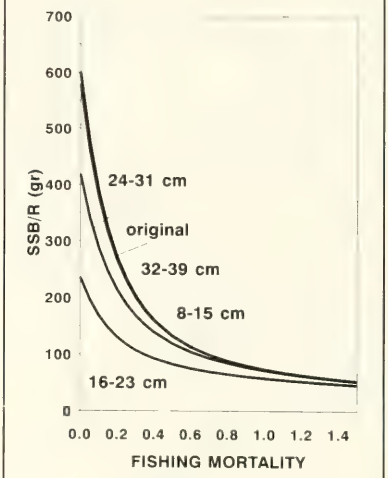

Figure 10

SSB/R for black sea bass *Centropristis striata* estimated under varying transition rates-at-length (L_c = 16 cm). Rates were increased 20% within each length-group indicated.

Table 3

SSB/R for black sea bass *Centropristis striata* as percentage of original values (and L_c=16 cm), where transformation rates have been doubled in differing 8 cm intervals.

F	8–15 cm	16–23 cm	24–31 cm	32–39 cm
0	99.7	39.1	69.5	96.3
0.1	99.7	43.3	74.0	97.2
0.2	99.7	47.9	78.6	98.0
0.3	99.7	52.8	82.9	98.6
0.4	99.7	57.6	86.6	99.1
0.5	99.7	62.1	89.6	99.4
0.6	99.8	66.1	92.0	99.6
0.7	99.8	69.7	93.9	99.8
0.8	99.8	72.9	95.3	99.9
0.9	99.8	75.7	96.4	99.9
1.0	99.8	78.2	97.2	99.9
1.1	99.8	80.4	97.9	100.0
1.2	99.8	82.4	98.4	100.0
1.3	99.8	84.2	98.7	100.0
1.4	99.9	85.8	99.0	100.0
1.5	99.9	87.2	99.2	100.0

were based on a target %MSP, the presence or absence of transition terms in the model would provide dramatically different interpretations. For instance, if the target %MSP were 30% with an F=0.8, and L_c=25 cm, the non-transitional model would indicate the situation was below the target at 22%, whereas the transitional model would place the current conditions above the target at 34%. It would be critical that calculation of SSB in the stock-recruitment relationship used for development of a target SSB/R (and associated %MSP) be made using a framework similar to calculation of SSB/R.

Beyond the issue of the model structure is the appropriateness of using spawning biomass models in general for management of hermaphroditic fishes. The complex social hierarchy of reef fishes (black sea bass can be considered a temperate reef fish) during spawning implies that the number of males may be an important factor limiting reproductive potential (Smith 1982). Recent theoretical studies suggest that males are not limiting in hermaphroditic sea bass populations to the degree that non-dominant males participate in spawning ("streakers") (Peterson 1991). If streakers are abundant, there would be no benefit for a female to transform only to engage in sperm competition with other spawning males. This suggests that under limited exploitation, the reproductive potential of the population is restricted in

terms of egg production. The possibility exists that exploitation could reach a level at which males are eliminated at such a rate that females are forced to transform faster or at an earlier size. The optimal sex ratio, from a behavioral perspective, has not yet been determined for *C. straita*. As suggested by the sensitivity analysis, substantial changes in the transformation rate could significantly alter the contributions of a cohort to the spawning biomass. There is no information currently available to determine the controlling mechanism or degree of plasticity for transformation rates within a population.

Future refinements of this distributed delay model may provide a more detailed picture of the effects of harvest on species such as black sea bass. Density-dependent feedback mechanisms influencing transition rates and age-at-first-transformation will ultimately be incorporated into the model to examine theoretical implications. A time-varying distributed delay model is also possible to account for seasonal changes in growth and mortality. With a minimal amount of growth information, either from back-calculations or tagging data, and some reasonable estimates of other important life-history events, we believe the distributed delay model can provide an effective length-based alternative to traditional dynamic pool models.

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Larval distribution patterns: Early signals for the collapse/recovery of Atlantic herring *Clupea harengus* in the Georges Bank area

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Abstract.—Changing temporal and spatial distribution patterns of Atlantic herring *Clupea harengus* larvae collected off southern New England over two decades provided early signals of large-scale changes in adult spawning biomass that are now a matter of record. Four contrasting spawning patterns were evident during the 20 yr period. Each pattern covered successive multiyear intervals and reflected the corresponding status of the adult population. In 1971, spawning occurred throughout the Georges Bank/Nantucket Shoals/Massachusetts Bay study area. The principal spawning grounds of herring in the Gulf of Maine region were located on the Northeast Peak of Georges Bank. With the collapse of the Georges Bank fishery in 1976, spawning receded westward to Nantucket Shoals. By 1979, larvae occurred only in the Stellwagen Banks area of Massachusetts Bay, the smallest of the three subareas. After a 6yr hiatus, spawning beds on Nantucket Shoals were reoccupied in 1985. By 1988 spawning had advanced eastward to Cultivator Shoals on Georges Bank, but through 1990 we found no evidence of renewed spawning activity on the historically-prominent spawning beds on Northeast Peak. The rebuilding process was attributed to recolonization rather than resurgence.

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The Atlantic herring *Clupea harengus* has been a target species of broad-scale early-life-history research in the Gulf of Maine since 1956. The initial larval surveys were part of a collaborative study by U.S. and Canadian biologists to define the stock structure of herring in the Northwest Atlantic (Tibbo et al. 1958). This effort continued over two spawning seasons and was followed by annual observations on distribution patterns of herring larvae during 1962–70 (Boyar et al. 1973b). Thereafter, U.S. biologists participated in a multinational field program that represented the starting point of the Northeast Fisheries Science Center's (NEFSC) current database for larval herring. This study, sponsored by the International Commission for the Northwest Atlantic Fisheries (ICNAF), was initiated in 1971 to identify mechanisms that influence survival of larvae (Lough et al. 1985).

With the termination of ICNAF larval herring surveys in 1977, NEFSC began a comprehensive fisheries ecosystem study of the Northeast Shelf Ecosystem (Sherman 1986, Smith 1988). This program, known as Marine Resources Monitoring, Assessment and Prediction (MARMAP), included standardized year-round surveys of fish eggs and larvae to provide baselines against which shifts in species composition and diversity within the finfish community could be observed and evaluated. These surveys continued for 11 years, ending in December 1987.

In 1988, ecosystems research emphasis at NEFSC shifted away from year-round surveys of the entire Northeast Shelf Ecosystem and focused on the Georges Bank area during autumn and winter. The new initiative was designed to document the changing status of herring and investigate density-dependent population regulation between herring and sand lance *Ammodytes* spp., important coastal pelagic species in the western North Atlantic. When combined, the three multi-year research endeavors conducted since 1971 provide an uninterrupted 20 yr database for larval herring in the Georges Bank/Nantucket Shoals/Massachusetts Bay area. During this period, dramatic changes occurred in the herring population.

Spawning biomass was relatively high at the onset of the ICNAF larval herring surveys in 1971, although in decline due to intense foreign fishing pressure that began in the mid 1960s. During the 1960s and continuing through the mid 1970s, biomass of herring on Georges Bank was estimated at 400,000–600,000 t. Annual catches ranged from 150,000 to 374,000 t. Dominating the population during the 1960s were three year-classes, 1956, 1960, 1961, and to a lesser extent 1966, although spawning success was poor in the closing years of the decade. Despite a strong 1970 year-class that entered the Georges Bank fishery in 1973, fishing

pressure by the large international fleet was so intense that landings declined after 1971. From 1973 to 1975 the principal herring landings shifted from the bank to the vicinity of Great South Channel, just east of Nantucket Shoals. After 15yr of moderate-to-heavy exploitation, and several years of quota management under ICNAF, the Georges Bank herring fishery collapsed in 1976 (Anthony & Waring 1980).

This paper examines the 20yr larval database to look for early signals of the dramatic changes in adult biomass that have occurred since 1971. We evaluate the influence of transport mechanisms on the spatial and temporal distribution patterns of larvae to corroborate the herring stock hypothesis of Iles & Sinclair (1982) and Sinclair & Iles (1985). Finally, we search for supporting evidence that the late-1980s recovery of herring in the Georges Bank area resulted from population resurgence rather than recolonization, a conclusion of Stephenson & Kornfield (1990).

Methods

The 20yr time-series began during the final years of the international fishery. It included a 10yr period when essentially no fishing took place in the study area, and ended with the 1990 spawning season when a limited fishery was again underway. Without a directed fishery after 1976, this dataset, along with NEFSC semi-annual trawl surveys, provided the only source of information to evaluate the status of herring in the Georges Bank area for more than a decade.

Sampling designs

All three larval surveys used the 61cm bongo, fitted with 0.333 and 0.505mm mesh nets. Larval herring catches from the 0.505mm net were analyzed. Net mesh selection was based on recommendations in Smith & Richardson (1977) and on Colton et al. (1980) who found no significant difference in retention rates of herring larvae captured in the two mesh sizes.

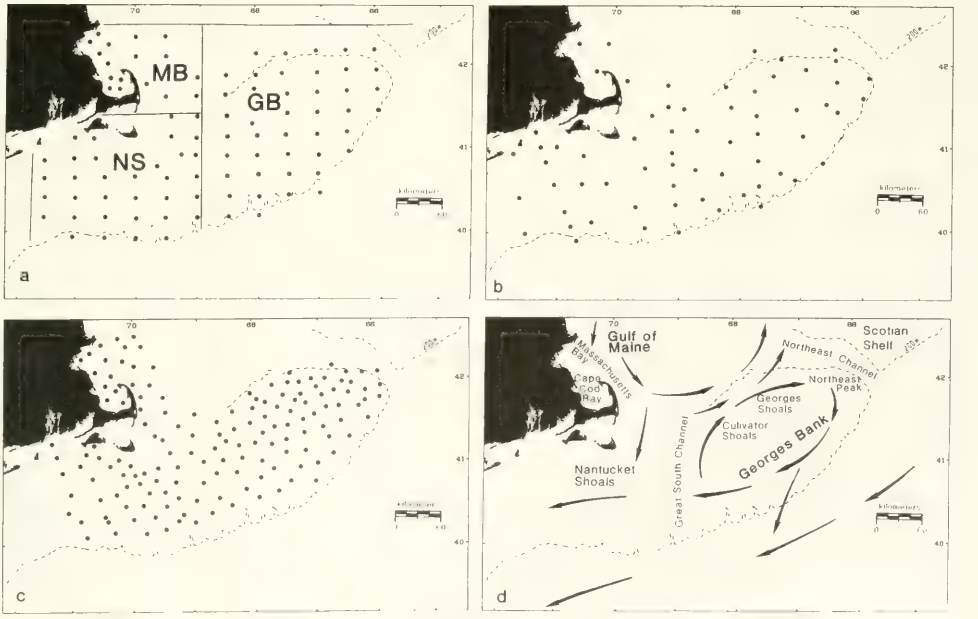

Figure 1

Station plan for **(a)** ICNAF larval herring surveys in the Georges Bank area, 1971–76, **(b)** MARMAP surveys in Georges Bank, 1977–87, and **(c)** studies of herring/sand lance interactions, 1988–90. **(d)** General surface circulation in the Georges Bank area (after Ingham 1982).

The ICNAF larval herring program included the entire Gulf of Maine region but concentrated on the Nantucket Shoals/Georges Bank area (Lough & Bolz 1979a, Lough et al. 1985). The 33 surveys conducted between 1971 and 1976 were used in our analysis. ICNAF participants deployed the bongo at 50 m/min to a maximum depth of 100 m and retrieved it in a smooth oblique profile at 10 m/min. Towing speed was 3.5 kn at stations spaced at 28–37 km intervals on a standard grid pattern (Fig. 1a). Additional stations in areas of high larval abundance were sampled after 1974. Lough & Bolz (1979b) provided a detailed account of sampling operations and cruises for the ICNAF time-series.

MARMAP surveys, conducted at monthly to bimonthly intervals, covered the continental shelf from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia. Cruise activities were described by Sibunka & Silverman (1984, 1989). MARMAP surveys fished the 61cm bongo to a maximum depth of 200 m with payout at 50m/min and retrieval at 20 m/min. Ship speed varied between 1 and 2 kn to maintain a 45° angle in the towing wire. Station intervals ranged from 15 to 45 km (Fig. 1b).

The herring recovery study initiated in 1988 employed MARMAP sampling methods. Cruises were conducted at about monthly intervals and occupied 151 stations in the Nantucket Shoals/Massachusetts Bay/Georges Bank study area (Fig. 1c).

Data analysis

We adjusted the number of larvae caught at each station in the time-series to reflect day/night/twilight catch differences (see Morse 1989). Larvae were partitioned into size-intervals to depict changes in distribution patterns over time. When the partitioned size-intervals of 4.0–7.9 mm, 8.0–12.9 mm, 13.0–17.9 mm, and >17.9 mm were corrected for shrinkage (see Theilacker 1980), they approximated age-groups of <2 wk, 2–5 wk, 5–8 wk, and >8 wk, respectively (Lough et al. 1982). Surveys were grouped by multi-year periods that represented time-intervals between the most apparent changes in spawning patterns during the 20 yr period. Figures showing mean numbers of larvae per 10 m^2 surface area were based on methods recommended for the delta distribution (Pennington 1983). Distributions of larvae grouped by age over time are discussed in relation to circulation patterns shown in Fig. 1d.

Results

Changes in distribution and abundance of herring larvae during the 20 yr time-series reflected four contrasting spawning patterns that spanned successive multi-year intervals. Larvae were abundant on both Nantucket Shoals and Georges Bank, but not so in Massachusetts Bay, during 1971–75. Conversely, we found low to no measurable numbers of larvae on Nantucket Shoals and Georges Bank during 1976–84, a period when spawning activity increased in Massachusetts Bay. Spawning resumed on Nantucket Shoals in 1985. During 1985–87, larval abundance peaked in Massachusetts Bay but the center of spawning activity shifted to Nantucket Shoals.

Herring were again spawning on the western half of Georges Bank in 1988. The dramatic increase in spawning activity on Nantucket Shoals and renewed spawning on western Georges Bank during 1988–90 elevated larval abundance estimates to their highest levels during the closing years of the time-series (Fig. 2).

When the time-series began in 1971, Georges Bank had been the principal spawning grounds for herring

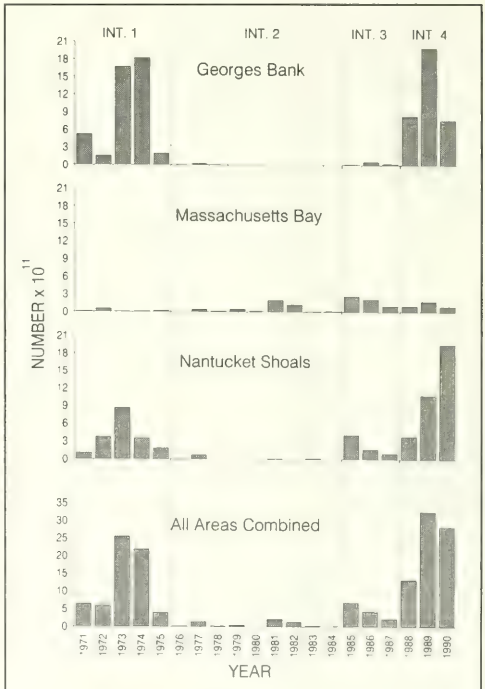

Figure 2

Changes in abundance of Atlantic herring *Clupea harengus* larvae by subarea during the 20yr time-series. Intervals (Int) represent multi-year periods that reflect the most apparent changes in spawning patterns.

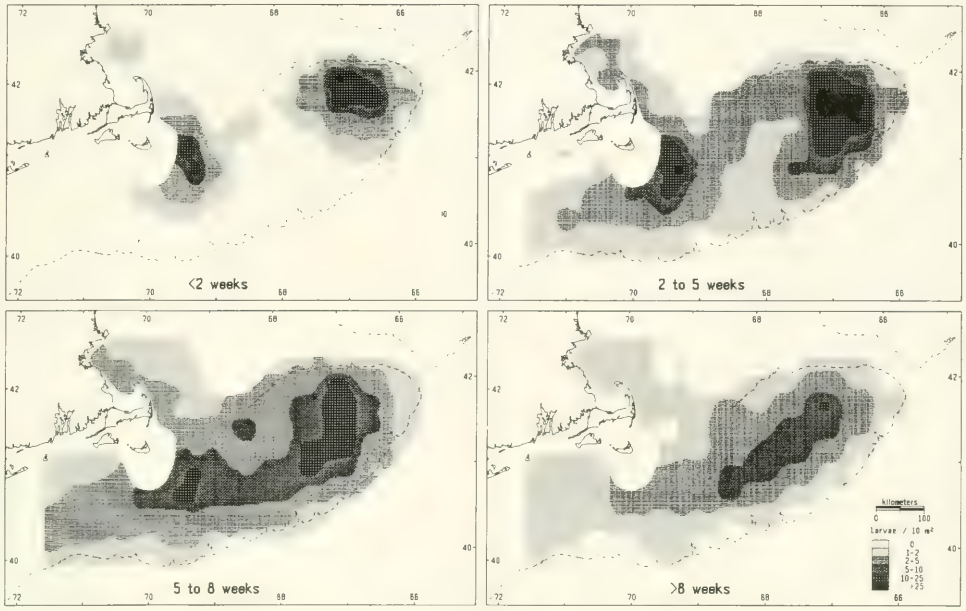

Figure 3
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1971–75.

in the western North Atlantic for at least 15yr (Tibbo et al. 1958, Boyar et al. 1973b, Anthony & Waring 1980, Lough et al. 1985, Grosslein 1987). The magnitude of spawning activity, as measured by the abundance of larvae, was low in 1971 and 1972 but increased sharply in 1973 and continued upward in 1974, the initial spawning years of the strong 1970 year-class. In 1975, larval abundance on Georges Bank declined dramatically and spawning activity on Nantucket Shoals equaled that on the bank. By 1976, when surveys showed only negligible spawning activity east of the 69° meridian, Georges Bank had lost its longstanding status as the principal spawning ground for herring in the western North Atlantic (Fig. 2).

ICNAF surveys of 1971–75 identified two geographically-separate spawning areas: one centered along the eastern edge of Nantucket Shoals, the other on northeastern Georges Bank (Fig. 3). Within 2–5 wk of hatching, larvae began to disperse and the two spawning centers were no longer discrete. At 5–8 wk after hatching, some larvae originating on the Northeast Peak were transported westward across the southern half of Georges Bank by anticyclonic currents. Together with larvae from Nantucket Shoals, their distribution extended over shelf waters from Cape Cod eastward and continued into adjacent slope waters. Although distributions of both Nantucket Shoals and Georges Bank larvae exhibited the influence of known circulation patterns within 5 wk of hatching (Fig. 1d), centers of abundance remained near their points of origin for at least 8 wk. Thereafter, a single center of abundance for larvae >8 wk old emerged over the shallow central part of Georges Bank (Fig. 3).

Herring larvae in all four age-groups occurred largely in coastal waters immediately adjacent to Cape Cod during the 1976–84 time-interval, a distribution pattern that differed significantly from those observed during the first 5yr of the time-series (Fig. 4). We found no larvae <2 wk old on Georges Bank in 1977. In 1978, only a few larvae in the youngest grouping were caught over the once-productive Northeast Peak. For the next decade, we caught no recently-hatched larvae anywhere on Georges Bank. Larvae <2 wk old were essentially absent on Nantucket Shoals during the 1976–84 time-interval as well. The center of larval abundance in each of the four groupings occurred in Massachusetts

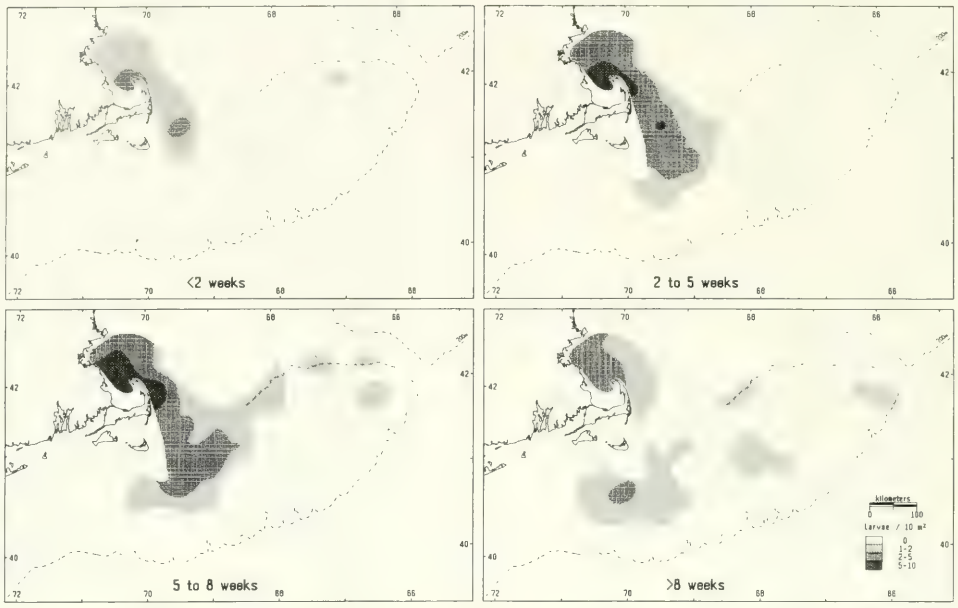

Figure 4
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1976–84.

and Cape Cod bays. As during the 1971–75 interval, larvae partitioned by age exhibited the influence of transport, especially in 1981 and 1982 when distribution patterns expanded from Massachusetts Bay to Nantucket Shoals. Averaging catches over a 9 yr period did not mask the effects of larval transport during the 1981 and 1982 spawning seasons (Fig. 4).

Further change marked the ensuing 3 yr period (1985–87), providing the first evidence that the herring population in the study area was beginning to recover. Spawning beds on Nantucket Shoals were reactivated in 1985, and the center of larval abundance shifted from Massachusetts Bay to Nantucket Shoals (Fig. 5). The influences of advective processes on the distribution of larvae were evident within a month after hatching. Nantucket Shoals larvae 2–5 wk old were transported by the Georges Bank gyre eastward across the northern part of the bank as far as the 68° meridian. The distribution pattern of 5–8 wk old larvae resembled that of 2–5 wk old fish, but exhibited the influence of further drift away from the Nantucket Shoals spawning beds. Larvae >8 wk old were caught in Massachusetts Bay and from Nantucket Shoals eastward onto Georges Bank. As in the 1976–84 period, no recently-hatched larvae occurred over the traditional spawning beds on eastern Georges Bank through 1987 (Fig. 5).

The reoccupation of spawning beds on the western half of Georges Bank and the increasing abundance of larvae on Nantucket Shoals during 1988–90 provided further signals of the changing status of herring in the study area (Fig. 6). Although the principal spawning grounds remained on Nantucket Shoals, the appearance of recently-hatched larvae on Georges and Cultivator shoals in all 3 yr provided the first evidence in a decade of spawning east of the 68° meridian on Georges Bank. Within 5 wk of hatching, larvae were dispersed over all but the eastern tip of the bank. By the time larvae reached 8 wk of age, they occurred throughout the study area (Fig. 6). As with the reactivation of Nantucket Shoals spawning beds in 1985, 3 yr lapsed from the time we first observed larval transport onto Georges Bank until we found evidence of spawning on the bank. Although the recovery of herring in the Georges Bank region was clearly underway during the closing years of the 1980s, we found no evidence in

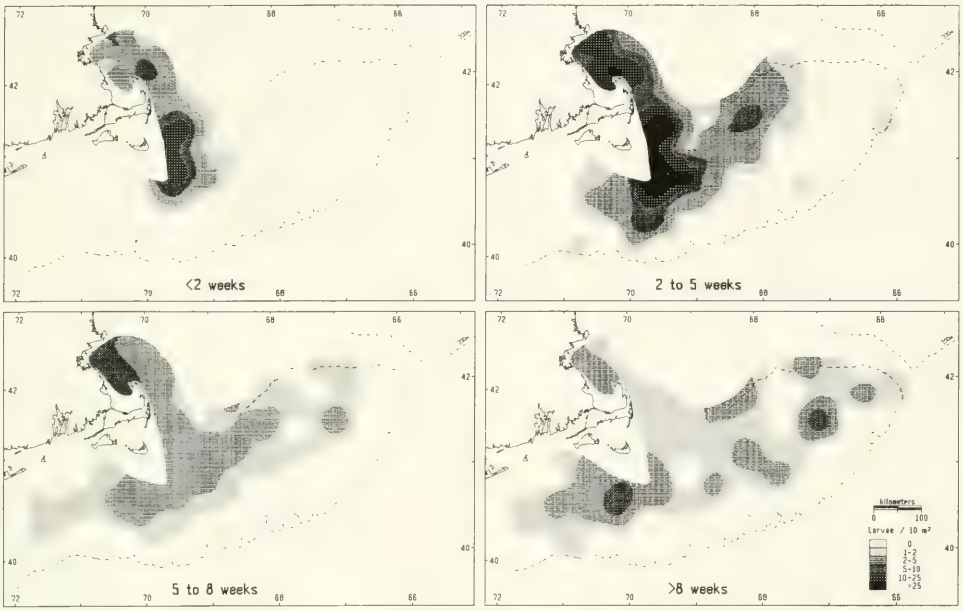

Figure 5
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1985–87.

larval distribution patterns through the 1990 spawning season that the historically prominent spawning beds on eastern Georges Bank had been reoccupied.

Discussion

The literature contains conflicting descriptions of the herring population structure in the western North Atlantic. Iles & Sinclair (1982) hypothesized that the number of Atlantic herring spawning stocks in the Gulf of Maine region is determined by the number of geographically-stable larval retention areas. They recognized four stocks: southwest Nova Scotia, Grand Manan, Georges Bank, and Nantucket Shoals. Sinclair & Iles (1985) revised the stock structure to include Jeffreys Ledge, coastal Gulf of Maine, and Scots Bay. Both Iles & Sinclair (1982) and Sinclair & Iles (1985) further hypothesized that (1) stocks are segregated only during autumn when herring return to their respective spawning grounds, (2) larvae of different stocks do not intermix for several months after hatching, the period when imprinting occurs, and (3) hydrographic conditions create retention areas by isolating larvae in vertically-mixed areas surrounded by stratified waters. Their retention hypothesis recognized that the geographic extent of the retention areas could vary annually and that some horizontal displacement could occur during larval development.

Grosslein (1987) reviewed the stock structure of herring in the Gulf of Maine region using the collective evidence from prior studies. He concluded that the population was composed of three major stocks: Georges Bank, western Nova Scotia, and the Gulf of Maine, with lesser spawning occurring elsewhere around the gulf. Grosslein indicated, however, that this breakdown was speculative and that direct attempts to differentiate between stocks through larval surveys, tagging studies, meristic and morphometric characters, biochemical methods, and parasitology produced inconclusive results.

Smith & Jamieson (1986) argued that no scientific basis existed for the stock concepts of Atlantic herring in either the eastern or western North Atlantic. They viewed the breakdown of herring stocks as transient subdivisions having no taxonomic or evolutionary

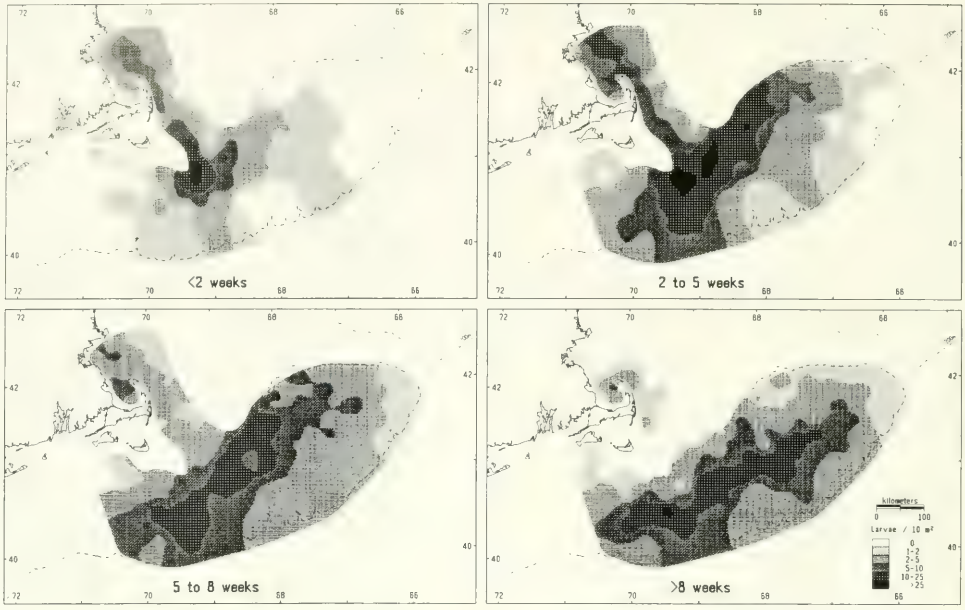

Figure 6
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1988–90.

status. Cushing (1986) also took exception to the retention hypothesis as applied by Iles & Sinclair (1982) to the North Sea area. Cushing (1986) noted that herring do not always spawn in transition zones around the British Isles and, where they do, the fronts brake down within a month after hatching. He further dismissed the retention concept by demonstrating that postlarval metamorphosis takes place near the nursery grounds after prolonged larval drift.

Our analysis of the 20 yr larval time-series supports that segment of the literature showing herring larvae vulnerable to advection after hatching (e.g., Cushing 1986, Bartsch et al. 1989, Heath & Walker 1987). Although transport in our dataset is not extensive, it is not restricted to the retention areas described by Sinclair & Iles (1985). Larvae drift from Massachusetts Bay southward to Nantucket Shoals, and the anticyclonic gyre on Georges Bank mixes larvae originating there with those spawned on the shoals. The direction of transport generally corresponds with reported circulation, a pattern consistent with that of Parrish et al. (1981). Mixing of larvae from the three subareas occurs within weeks after hatching, or earlier in the life cycle than proposed by Sinclair & Tremblay (1984) and Sinclair & Iles (1985).

Drift trajectories of herring larvae from other studies in the Gulf of Maine region agree with our findings in that they correspond to dominant circulation patterns described by Ingham (1982) and Butman & Beardsley (1987). Graham et al. (1972) and Graham (1982) recognized that some herring larvae spawned off eastern Maine drifted westward to mix with larvae originating in central and western Maine waters. Townsend et al. (1986) provided further evidence that herring larvae off Maine are advected from east to west. Although Chenoweth et al. (1989) noted that residual currents do not demonstrate a persistent flow in any direction off eastern Maine, they too observed a westward displacement of herring larvae. Finally, Boyar et al. (1973a) showed herring larvae spawned on Jeffreys Ledge, another of the retention areas of Sinclair & Iles (1985), drifting into Massachusetts Bay where they could mix with larvae originating on and around Stellwagen Bank. Given these reports of drift and mixing in western Gulf of Maine waters near our study area and the demonstrated dispersion and

mixing of early-stage larvae reported here, we see no compelling argument for the separation of herring stocks through larval retention in the western Gulf of Maine and Georges Bank areas.

We consistently found sufficient larval drift and mixing to question the stock structure of Sinclair & Iles (1985) in the Georges Bank region. However, Figs. 3–6 lend some support to the retention hypothesis by showing that a significant portion of the larvae up to 8wk old remained near their points of origin. Campana et al. (1989a, 1989b) reported similar results for haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* larvae, respectively, on Browns Bank. Some larvae of the two species were transported shoreward while others remained near the spawning grounds longer than known water residence time. Both of the 1989 studies concluded that the instability of the Browns Bank gyre accounted for the dichotomous distribution patterns. They interpreted the onshore drift as an all-or-none situation for individual larvae. Some readily exited the influence of a weakly established gyre, while most were retained during periods of pronounced gyral circulation. In our view, their theory provides a more plausible explanation for the shifting distribution patterns of herring larvae around Georges Bank, an area also influenced by gyral circulation, than the stock hypothesis proposed by Iles & Sinclair (1982).

Stephenson & Kornfield (1990) attributed the increasing biomass of herring on Georges Bank during the late 1980s to the resurgence of residual fish rather than to recolonization by fish from surrounding areas. Based largely on a 4 yr dataset that excluded Nantucket Shoals and Massachusetts Bay, they concluded that (1) adult herring caught on Georges Bank differed in age composition from herring on Jeffreys Ledge and southwestern Nova Scotia, (2) some of the Georges Bank herring exhibited different isoenzyme characteristics than neighboring herring, and (3) the return of herring to Georges Bank took longer than they expected through recolonization.

In our view, the change in spawning sites on Georges Bank during the 20 yr time-series, coupled with the recession and subsequent expansion of the spawning range over time, makes a convincing case for recolonization rather than resurgence. Larval distribution patterns on Georges Bank during the closing years of the time-series differed markedly from those observed at the outset of the program. Whereas recently-hatched larvae were concentrated on Northeast Peak during the initial survey years, their distribution on the bank progressed eastward only as far as Georges Shoals during the final years of survey activity. If, as proposed by Stephenson & Kornfield (1990), resurgence of residual fish accounted for the recovery of spawning herring on the bank, we would expect little or no change in the location of spawning centers over time. Instead, our 20 yr time-series shows dramatic change.

When the herring population in the study area declined in the early 1970s, its spawning range receded from Georges Bank to Massachusetts Bay. As the population began to grow in the 1980s, the spawning range expanded, initially from Massachusetts Bay to Nantucket Shoals, then from the shoals to Georges Bank. Whether the recovery resulted from an expanding adult population, from fortuitous transport and survival of larvae, or from a combination of the two, is not clear. However, it is worth noting that the reoccupation of spawning beds on both Nantucket Shoals and Georges Bank occurred 3–4 yr after we first observed evidence of larval drift towards these two subareas. This time period, perhaps coincidently, represents the age-at-maturity for Atlantic herring.

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Relative abundance of pelagic resources utilized by the California purse-seine fishery: Results of an airborne monitoring program, 1962–90

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Abstract. – During the period 1962–90, an aerial monitoring program conducted in cooperation with aerial spotters searching for pelagic fishes off California and Baja California, Mexico resulted in the development of an index of apparent abundance for six species of fishes: the northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific bonito *Sarda chiliensis*, Chub mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, and bluefin tuna *Thunnus thynnus*. Northern anchovy was the dominant species observed, accounting for 89.7% of tonnage recorded during 1962–90. Chub mackerel comprised 6.1% of the total tonnage, jack mackerel 2.1%, Pacific sardine 1.0%, Pacific bonito 0.6%, and bluefin tuna 0.5%.

Apparent abundance indices were computed by dividing the tonnage observed by the number of "block areas" (10' lat. × 10" long.) searched, expressed as tons/block area flown (T/BAF). Indices were calculated for the total area and for the core area of distribution and abundance for each species. All species exhibited large fluctuations in apparent abundance over time. The apparent abundance index for Pacific sardine declined to a very low level during 1966–83. A substantial increase in abundance occurred during the mid- to late-1980s, with the 1990 index value 58 times that observed during the early 1960s. The chub mackerel abundance index declined to a very low level during 1966–76, then increased to a record high value in 1978 and has since declined. The northern anchovy abundance index increased in the early 1970s, with high abundance levels recorded during 1972–81, and then declined sharply to very low levels in the 1980s. The Pacific bonito abundance index was high during 1965–67 and 1983–85, with current levels well below the long-term mean. Very high abundance index levels for jack mackerel were recorded during 1975–79, then declining to very low levels in the 1980s. The bluefin tuna abundance index increased during 1972–80, declining to very low index values since. Based on these data, several species appear to be fluctuating unpredictably with respect to species abundance over time.

Aerial indices were compared with available total, spawning, and larval biomass estimates developed for several species. The most significant correlation of the aerial index was between the northern anchovy and Pacific sardine larval indices.

The rapid decline of the Pacific sardine *Sardinops sagax* fishery in the late 1940s resulted in increased research by the State of California Department of Fish and Game (CDF&G), Federal Government, and other institutions to determine the underlying principles that govern the sardine's behavior, availability to the fishery, and total abundance (Clark & Marr 1955, Sette 1969, Radovich 1982). Catch-per-unit-effort (CPUE) studies of the sardine purse-seine fishery off California did not indicate a significant decline in abundance until just prior to the fishery collapse (Fox 1974). Fisheries tend to target their fishing effort in areas of high densities of fishes (Radovich 1982, Squire & Au 1990), hence CPUE may not accurately reflect resource abundance (de La Mare 1984; J.B. Phillips, CDF&G, pers. commun., 1954). Clark & Marr (1955) concluded that, in addition to other information needs, better information is needed on changes in availability of sardine to the fishery. Related to this is the need for better real-time measures of trends in apparent abundance for successful management of pelagic schooling resources.

In the mid-1950s, the use of aircraft in searching and fishing operations of the California purse-seine fleet had become well established, as was the case in many other U.S. fisheries (Squire 1961). Having had experience in conducting commercial aerial fish spotting and several aerial fish-resource surveys, I initiated a pelagic monitoring program in the fall of 1962, with the cooperation of aerial fish-spotter pilots searching for fish for the commercial purse-seine fishery off central and southern California. The purpose of the program was to develop an effective method of measuring apparent abundance and monitoring changes in abundance. In the case of aerial observations, the concentrations of fish observed may or may not be subjected to fishing.

This paper updates the analysis of apparent abundance data collected by the aerial monitoring program from the first full year of data, 1963–90, using different analytical methods than used in earlier papers (Squire 1972, 1983). It also reviews the trends in apparent abundance during the period 1963–90 for six pelagic species by geographical area and compares the relation of the aerial abundance estimates to other independent biomass estimates made for the same species. The term "apparent abundance" (Marr 1951) refers to that portion of total abundance that is available to the fishery.

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Species included in this study are the northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific bonito *Sarda chiliensis*, chub mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, and bluefin tuna *Thunnus thynnus*. These species, along with market squid *Loligo opalescens*, are the primary targets of the commercial purse-seine fleet based in San Pedro, California. Most are also fished by the southern California sportfishing fleet. The species are members of a complex interacting coastal and oceanic ecosystem that crosses international boundaries (Sette 1969).

Methods

Procedures for collection and tabulation of data

Since the fall of 1962, fish-spotter pilots have been directed to complete a flight logchart at the termination of each spotting flight. These pilots were instructed to draw their flight track on the chart and record the locations of all schools of fish species observed, along with their best estimates of tonnage observed. These data were recorded either as total tonnage of fish in

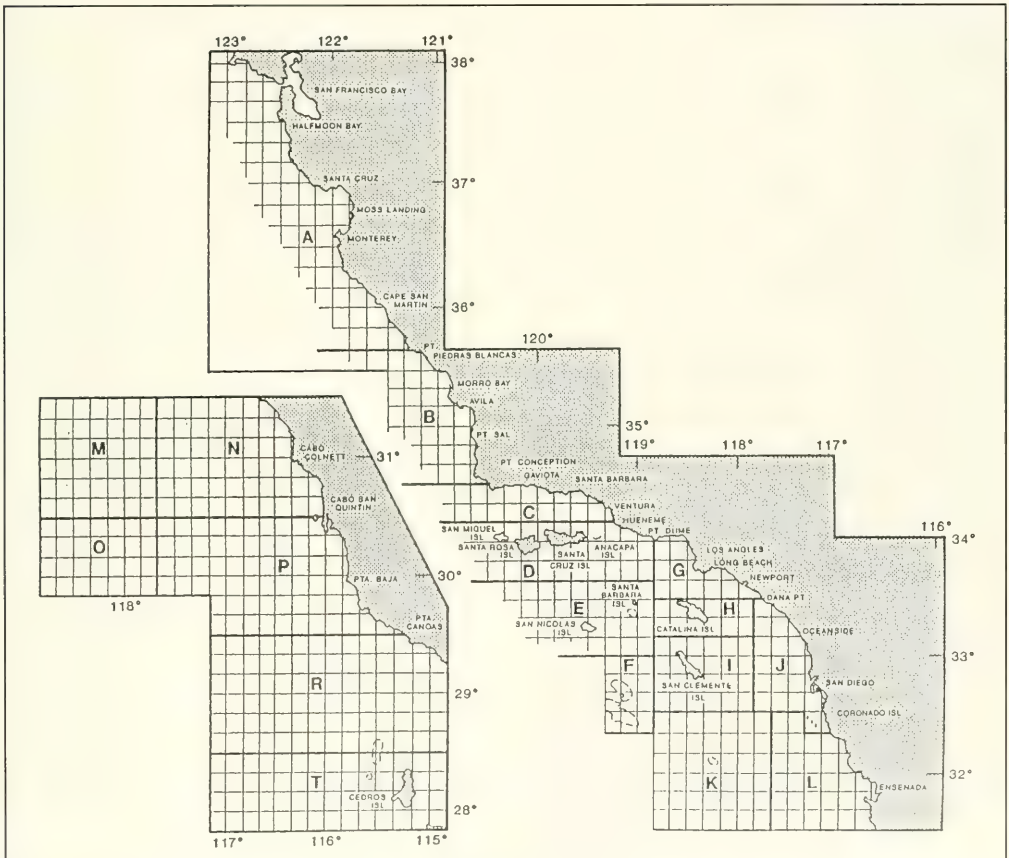

Figure 1

Block areas designated for sampling from off central California to Mexico, grouped in 18 zones, A to T. (Zones Q and S were originally used on flight logs; however, no flights were recorded for these zones.)

the area or numbers of schools with an estimate of the tonnage of each school. Procedures for recording species observations and survey effort have not changed since 1962. Other information such as time of flight (day or night) and flight duration also are recorded on the flight log. Flight logs are submitted quarterly and data from each log are entered into the computer after editing.

Spotter pilots' income is derived from the commercial fishery at a current rate of ~6% of the vessel's gross income. Spotter pilots are paid a nominal fee by the National Marine Fisheries Service (NMFS) to maintain a flight log record of their observations. Pilots in the program averaged ~600h flight time/yr and, with 4–6 pilots, the total number of hours flown was ~3000/yr.

From 1963, the first full year of operation, to 1990, annual indices of abundance for each species were calculated for the total area (from northern Baja California, Mexico to San Francisco, California) and for selected groups of 10" lat. × 10" long. block areas, similar to the "block area" statistical system used by CDF&G (Anon. 1935). These groups of block areas are referred to in this paper as "zones" and were designed to encompass important commercial fishing areas (Fig. 1).

Flight effort for the total area and each zone was determined by counting the number of times the aerial spotter's flight track entered a block area, termed a "block area flight" (BAF). Species abundance was recorded as the tonnage estimate (and hence approximates biomass) for the area observed. Also recorded on the flight log was time of the observation (day or night), pilot, and, since 1988, the target species of the commercial operation.

The procedure to measure effort has not changed from previous studies; however, the computation of species abundance has been modified. In previous analyses (Squire 1972, 1983), abundance was estimated as a rank index according to discrete incremental values of tonnage (tonnage range values). For example, for the northern anchovy, an observation within a block area estimated to be 0–100t was recorded as 1, 100–200t was recorded as 2, etc. Each species had different tonnage range values, since the amount of tonnage observed varied greatly between species. Therefore, the abundance index values for each species are not directly comparable. For this analysis, actual tonnage values as recorded by the spotter pilot and a modification of the index used by Squire (1972) are used, which allows for direct comparison of abundance index values between species.

The apparent abundance index is T/BAF, where T = tonnage estimate, and BAF = total number of block area flights (day plus night, all zones).

Results and discussion

Observation effort and sightings

During the period 1963–90, a total of 24 aerial fish-spotter pilots participated in the program and reported flight operations totaling over 67,000h, searching a total of 376,446 block areas. Table 1 gives the annual search effort (BAF/yr), day and night, during the period 1962–90. From 1963 to 1990, a total of 253,239 BAF were made during day operations (67%) and 123,207 BAF during the night. Pilots have searched an average of 13,444 BAF/yr; however, the variation in annual spotting effort is considerable. There was reduced effort in early 1970. Abundance data for 1970

Table 1

Search effort in block area flights (BAF), day and night, 1963–90, from off Baja California, Mexico to central California. Asterisk indicates <1/2 yr of operation.

	Block area flights		
Year	Day	Night	Total
1962*	362	512	874
1963	3,541	3,279	6,820
1964	5,245	3,415	8,660
1965	5,086	4,367	9,453
1966	7,708	3,781	11,489
1967	7,632	3,495	11,127
1968	7,823	3,835	11,658
1969	9,745	5,896	15,641
1970	4,646	1,853	6,499
1971	12,308	5,181	17,489
1972	7,402	4,448	11,850
1973	12,450	5,031	17,481
1974	8,356	3,887	12,243
1975	7,923	3,398	11,321
1976	14,782	3,781	18,563
1977	7,795	7,788	15,583
1978	6,517	4,415	10,932
1979	10,727	4,767	15,494
1980	3,624	3,403	7,027
1981	9,237	3,781	13,018
1982	9,597	5,754	15,351
1983	13,904	4,571	18,475
1984	9,144	1,063	10,207
1985	15,243	4,031	19,274
1986	12,300	5,684	17,984
1987	8,474	6,348	14,822
1988	7,185	3,335	10,520
1989	8,744	4,116	12,860
1990	16,101	8,504	24,605
Total 1963–90	253,239 = 67%	123,207 = 33%	376,446

Avg. = 13,444 BAF/yr, 1963–90

Table 2
Sighting estimates of total tonnage by species and percentage and by zones, for the period 1962–90.

Zone	Northern anchovy	Pacific sardine	Pacific bonito	Chub mackerel	Jack mackerel	Bluefin tuna
A	25,147,498	19,157	674	108,345	56,158	0
B	865,308	2,739	4,690	216,873	98,035	0
C	11,633,297	*614,595*	*233,330*	*1,386,548*	104,949	333
D	5,126,158	345,360	86,860	639,099	268,823	1,938
E	467,400	22,454	3,688	203,190	45,937	2,934
F	358,614	50,130	250	701,416	*789,877*	22,773
G	*28,519,793*	99,587	37,176	521,732	361,180	3,154
H	5,292,980	183,500	26,363	1,145,839	222,005	1,785
I	1,578,398	33,165	26,231	1,292,866	256,731	27,938
J	10,453,074	68,243	205,553	130,471	30,855	26,494
K	242,164	1,200	2,045	525	910	79,846
L	1,215,269	0	28,418	1,365	50	86,521
M	500	0	0	0	0	9,603
N	2,495,734	4,200	13,881	24,650	0	*143,625*
O	0	0	0	0	0	0
P	123,305	0	2,313	400	0	64,423
R	1,110	0	0	0	0	8,652
T	0	0	0	0	0	0
	93,520,602	1,444,321	671,472	6,373,169	2,235,510	480,019
%	89.7	1.0	0.6	6.1	2.1	0.5

Table 3
Day/night sighting estimates for northern anchovy, Pacific sardine, Pacific bonito, Pacific mackerel, jack mackerel and bluefin tuna, 1962–90.

	Day	Night
Northern anchovy *Engraulis mordax*		
Tonnage	30,140,974	63,379,618
% day/night	32.3	67.7
Pacific sardine *Sardinops sagax*		
Tonnage	361,548	1,082,498
% day/night	25.1	74.9
Pacific bonito *Sarda chiliensis*		
Tonnage	521,302	151,169
% day/night	77.5	22.5
Pacific mackerel *Scomber japonicus*		
Tonnage	2,534,780	3,837,366
% day/night	39.8	60.2
Jack mackerel *Trachurus symmetricus*		
Tonnage	746,827	1,488,683
% day/night	33.5	66.5
Bluefin tuna *Thunnus thynnus*		
Tonnage	462,262	17,756
% day/night	96.3	3.7

are thus not directly comparable to other years, although most search effort was during a period of high abundance levels. Through the years, the center of search effort was off southern California, with search activity off northwestern Baja California, Mexico during the summer for bluefin tuna. There was considerable search effort north of Point Conception into the Monterey Bay area for chub mackerel and Pacific sardine during the early years of the program and less so since the decline in those species' abundances in the mid-1960s.

Estimates of total tonnage sighted by species by zone are given in Table 2. The tonnage estimated for northern anchovy far exceeds that of all other species, totaling 89.7%. The greatest tonnage of northern anchovy was observed in zone G; Pacific sardine, Pacific bonito, and chub mackerel in zone C; jack mackerel in zone F; and bluefin tuna in zone N.

Most spotting effort was carried out during summer to fall, with 49% of BAFs accounted for during the months of July, August, and September (1980–90). During any one year, the amount of effort expended in any one month was highly variable due to fluctuations in abundance, weather, and fleet operations. In summer months, a substantial portion of the increase in spotting effort is related to searching for bluefin tuna, or other species such as albacore *Thunnus alalunga* and yellowfin tuna *Thunnus albacares*.

Differences in tonnage sighted between day and night (Table 3) are similar to that reported by Squire (1972). Northern anchovy, Pacific sardine, chub mackerel, and jack mackerel were more commonly observed at night, while Pacific bonito and bluefin tuna were more commonly observed during the day.

Table 4

Total area index values in T/BAF, day plus night. Dash indicates an abundance level <0.01 T/BAF.

Year	Total area	Year	Total area
Northern anchovy *Engraulis mordax*			
1962	0.66	1977	713.80
1963	141.38	1978	340.19
1964	80.66	1979	382.83
1965	153.45	1980	322.01
1966	83.26	1981	89.87
1967	163.63	1982	42.78
1968	72.20	1983	4.17
1969	195.82	1984	4.54
1970	608.43	1985	27.24
1971	195.63	1986	7.55
1972	81.05	1987	20.67
1973	745.98	1988	42.90
1974	354.25	1989	16.05
1975	819.93	1990	11.96
1976	293.77		
Pacific sardine *Sardinops sagax*			
1962	—	1977	—
1963	0.77	1978	—
1964	0.90	1979	—
1965	0.04	1980	—
1966	0.02	1981	0.01
1967	—	1982	0.12
1968	—	1983	0.15
1969	—	1984	1.88
1970	—	1985	34.37
1971	—	1986	19.87
1972	—	1987	11.76
1973	—	1988	77.11
1974	—	1989	6.23
1975	—	1990	11.83
1976	—		
Pacific bonito *Sarda chiliensis*			
1962	1.18	1977	0.14
1963	6.28	1978	4.35
1964	2.32	1979	0.31
1965	3.47	1980	0.33
1966	10.16	1981	1.73
1967	5.34	1982	0.38
1968	3.06	1983	0.96
1969	1.50	1984	8.17
1970	0.87	1985	3.22
1971	2.93	1986	0.22
1972	2.28	1987	1.55
1973	2.98	1988	1.55
1974	1.40	1989	0.98
1975	0.48	1990	0.76
1976	0.43		
Pacific mackerel *Scomber japonicus*			
1962	2.74	1977	72.30
1963	6.62	1978	142.26
1964	1.06	1979	63.75
1965	0.11	1980	39.10
1966	0.23	1981	31.59
1967	—	1982	26.71
1968	—	1983	8.89
Pacific mackerel *Scomber japonicus* (continued)			
1969	0.03	1984	72.44
1970	0.83	1985	88.73
1971	0.13	1986	41.77
1972	0.03	1987	17.38
1973	0.18	1988	21.66
1974	—	1989	3.53
1975	0.02	1990	3.18
1976	0.47		
Jack mackerel *Trachurus symmetricus*			
1962	5.04	1977	60.40
1963	13.73	1978	82.54
1964	11.56	1979	19.13
1965	9.97	1980	9.23
1966	2.70	1981	4.42
1967	6.61	1982	6.15
1968	11.41	1983	1.56
1969	3.55	1984	1.82
1970	1.87	1985	1.61
1971	5.91	1986	1.44
1972	6.27	1987	1.01
1973	0.21	1988	0.47
1974	1.88	1989	1.37
1975	5.69	1990	0.23
1976	3.89		
Bluefin tuna *Thunnus thynnus*			
1962	4.40	1977	7.12
1963	6.81	1978	30.07
1964	6.81	1979	12.32
1965	0.90	1980	0.69
1966	9.46	1981	0.80
1967	3.42	1982	0.80
1968	6.03	1983	0.20
1969	0.39	1984	0.66
1970	0.02	1985	2.57
1971	0.42	1986	3.03
1972	2.75	1987	0.55
1973	16.45	1988	0.56
1974	17.28	1989	0.48
1975	2.54	1990	0.35
1976	13.20		

Indices of apparent abundance

Abundance index levels in tons/block area flight (T/BAF) were calculated for the total area by species for day plus night observations for the years 1962–90 (Table 4). From the total area index, the general trend of species abundance can be obtained. However, an index designed to better represent abundance change of each species is needed; therefore, a second set of abundance index values was calculated using only data from a core area of abundance as determined for each species by day or night, depending upon which period best represented the abundance of the species (Squire 1972). With the exception of data from one aerial spotter pilot (computer file 26), all data collected during 1962–90 was used in this analysis.

Data reflecting number of sightings and tonnage observed and its geographical distribution were used to define the geographical limits of the core area for each species. The core area for each species was determined to include all or portions of the following zones: northern anchovy, zones C,D,G,H; Pacific sardine, zones C,D,G,H; Pacific bonito, zones C,D,G,J; chub mackerel, zones C,D,G,H,I; jack mackerel, zones D,F,G,H,I; bluefin tuna, zones I,K,L,N,P (Fig. 1). For each species, the number of block areas in each zone comprising its core area and the total number of block areas in its core area are given in Table 5.

The core-area index is the mean of the T/BAF weighted to account for differences in size of core area within the zone to obtain a stratified mean (Cochran 1966). For each zone, the weight factor was the ratio of the total number of block areas having high species density in the zone to the total number of block areas

Table 5

Areas of high density determining core-area abundance, by species.

Core area determined for		
Northern anchovy	Zone G =	10 block areas
Engraulis mordax	D =	11 " "
	C =	10 " "
	H =	6 " "
		37 block areas comprising the anchovy core area
Pacific sardine	Zone C =	6 block areas
Sardinops sagax	D =	5 " "
	G =	5 " "
	H =	4 " "
		20 block areas comprising the Pacific bonito core area
Pacific bonito	Zone C =	6 block areas
Sarda chiliensis	D =	8 " "
	G =	8 " "
	J =	7 " "
		29 block areas comprising the Pacific bonito area
Chub mackerel	Zone G =	6 block areas
Scomber japonicus	H =	3 " "
	I =	3 " "
	D =	5 " "
	C =	4
		21 block areas comprising the Pacific mackerel core area
Jack mackerel	Zone D =	8 block areas
Trachurus symmetricus	G =	7 " "
	H =	3 " "
	I =	3 " "
	F =	4 " "
		25 block areas comprising the jack mackerel core area
Bluefin tuna	Zone I =	20 block areas
Thunnus thynnus	L =	20 " "
	K =	15 " "
	N =	18 " "
	P =	8 " "
		81 block areas comprising the bluefin tuna core area

with high density comprising the entire core area. Core-area abundance (weighted T/BAF) is

$$\sum w_i (t/BAF)_i,$$

where W_i – weight for zone i = a/b

a = blocks in core area from zone i

b = total blocks in core area, all zones

$(T/BAF)_i$ = T/BAF for zone i.

Abundance trends by species

Core-area index values in Figs. 2–7 are presented as a weighted mean index and as a running average of three to better illustrate trends in abundance. Core-area abundance index values are given in Table 6.

Table 6

Core-area index values in T/BAF, day or night in T/BAF. Dash indicates an abundance level <0.01 T/BAF.

Year	Core area	Year	Core area
Northern anchovy *Engraulis mordax*			
1962	0.09	1977	858.73
1963	250.98	1978	263.89
1964	160.55	1979	624.80
1965	253.85	1980	578.68
1966	116.92	1981	236.71
1967	225.70	1982	67.86
1968	173.41	1983	7.72
1969	309.84	1984	6.76
1970	629.03	1985	47.88
1971	362.59	1986	13.39
1972	54.55	1987	33.28
1973	1143.55	1988	69.20
1974	494.29	1989	7.24
1975	1010.70	1990	31.45
1976	456.10		
Pacific sardine *Sardinops sagax*			
1962	—	1977	—
1963	1.38	1978	—
1964	1.31	1979	—
1965	0.02	1980	—
1966	0.03	1981	—
1967	225.70	1982	0.24
1968	0.01	1983	0.33
1969	—	1984	2.77
1970	—	1985	97.36
1971	—	1986	32.35
1972	—	1987	20.12
1973	—	1988	145.75
1974	—	1989	34.84
1975	—	1990	39.03
1976	—		
Pacific bonito *Sarda chiliensis*			
1962	2.20	1977	0.23
1963	2.29	1978	0.96
1964	3.39	1979	0.38
1965	5.88	1980	0.38
1966	14.84	1981	1.78
1967	7.20	1982	0.56
1968	3.35	1983	1.31
1969	1.58	1984	9.93
1970	—	1985	3.98
1971	3.47	1986	0.30
1972	2.83	1987	1.05
1973	3.34	1988	2.42
1974	1.76	1989	1.23
1975	0.74	1990	1.15
1976	0.59		
Chub mackerel *Scomber japonicus*			
1962	4.04	1977	104.80
1963	3.36	1978	198.72
1964	1.63	1979	85.27
1965	0.80	1980	58.78
1966	0.51	1981	41.74
1967	0.01	1982	29.24
1968	0.01	1983	19.00
1969	0.07	1984	59.91
1970	2.95	1985	148.18
1971	0.33	1986	85.48
1972	0.10	1987	36.06
1973	0.48	1988	43.55
1974	—	1989	7.83
1975	—	1990	3.19
1976	0.05		
Jack mackerel *Trachurus symmetricus*			
1962	5.28	1977	91.41
1963	23.10	1978	74.90
1964	14.69	1979	20.13
1965	14.58	1980	12.25
1966	4.49	1981	7.77
1967	15.26	1982	10.14
1968	24.21	1983	2.20
1969	5.68	1984	7.47
1970	2.91	1985	6.23
1971	12.55	1986	2.63
1972	11.65	1987	1.69
1973	0.39	1988	1.03
1974	3.41	1989	2.86
1975	13.17	1990	0.81
1976	11.59		
Bluefin tuna *Thunnus thynnus*			
1962	6.57	1977	8.71
1963	6.97	1978	34.52
1964	6.97	1979	12.87
1965	1.28	1980	0.89
1966	13.03	1981	0.95
1967	4.51	1982	1.37
1968	9.45	1983	0.05
1969	0.59	1984	0.62
1970	—	1985	2.32
1971	0.87	1986	1.98
1972	6.94	1987	0.77
1973	17.38	1988	1.23
1974	18.32	1989	1.02
1975	2.60	1990	0.73
1976	13.73		

Northern anchovy (Fig. 2) The core area index (night index) was near 180 T/BAF in the mid- to late-1960s. The index increased in the early 1970s, and during 1972–80 remained in the range of 450–700 T/BAF. The index began to decline in 1980 and reached a low level of abundance by 1983 (<50 T/BAF), a level considerably below that observed in the mid-1960s.

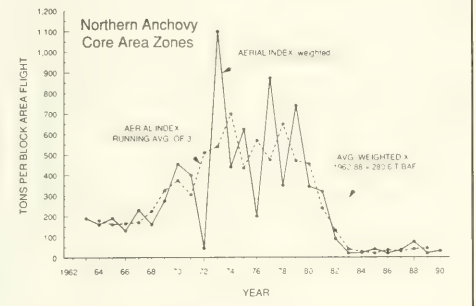

Figure 2
Abundance index levels in T/BAF for northern anchovy *Engraulis mordax* core area, night index, weighted $\bar{x}$, and running average (×3).

Pacific sardine (Fig. 3) The Pacific sardine resource was in a state of decline at the time the aerial spotter program was started. Average tonnage calculated for the 1963–66 period for the core-area index was 1.03 T/BAF. Very low abundance indices were recorded from 1967 until the early 1980s with some years reporting zero sightings of sardine schools. The core-area running mean index (night index) increased to 60 T/BAF by 1988.

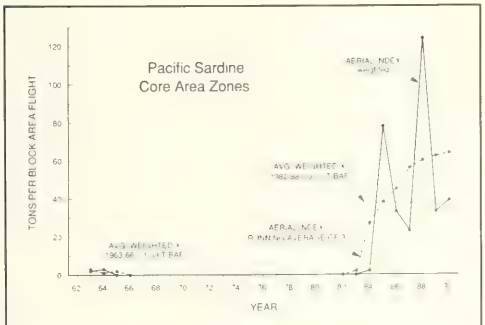

Figure 3
Abundance index levels in T/BAF for Pacific sardine *Sardinops sagax* core area, night index, weighted $\bar{x}$, and running average (×3).

Pacific bonito (Fig. 4) Abundance levels for Pacific bonito show considerable fluctuation. Bonito were rarely taken off southern California prior to the strong El Niño of 1957–58 (Radovich 1960). They were common in southern California waters after this event and were intensively fished starting in about 1963. The increase in fishing effort redirected to this species was the result of decreased abundance of Pacific sardine and chub mackerel.

The core-area index value (day index) reached a high in 1966 of 10.5 T/BAF. This is the highest index value recorded for bonito during 1962–90. The index then declined, increased slightly in 1972 to 3.2 T/BAF, and substantially increased in 1984 to 5.5 T/BAF.

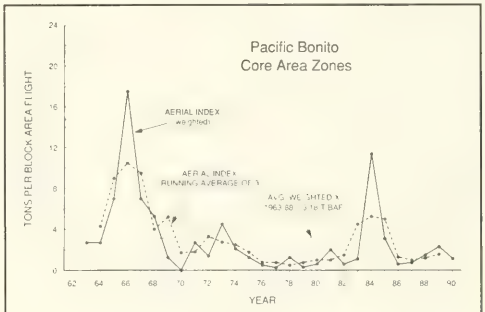

Figure 4
Abundance index levels in T/BAF for Pacific bonito *Sarda chiliensis* core area, day index, weighted $\bar{x}$, and running average (×3).

Chub mackerel (Fig. 5) Declining abundance levels noted in the early to mid-1960s matched the collapse of the fishery, with extremely low index levels (>5 T/BAF) noted for the core-area index (night index) in 1967–75. After 1976, the abundance index rose rapidly to a peak of 170 T/BAF in 1978, then declined to a range of 15–55 T/BAF in 1981–89.

Jack mackerel (Fig. 6) Abundance was high during the mid 1970s. The core-area index (night index) increased to 234 T/BAF in 1976 and declined to <10 T/BAF after 1979.

Bluefin tuna (Fig. 7) For the core area, there were three peaks in the index (day index) of abundance: 1967, 1973, and 1978. The index for recent years is well below the 1963–88 average of 10.8 T/BAF.

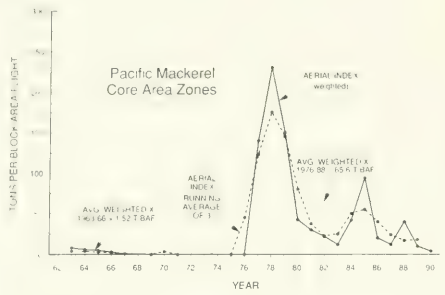

Figure 5

Abundance index levels in T/BAF for chub mackerel *Scomber japonicus* core area, night index, weighted $\bar{x}$, and running average (×3).

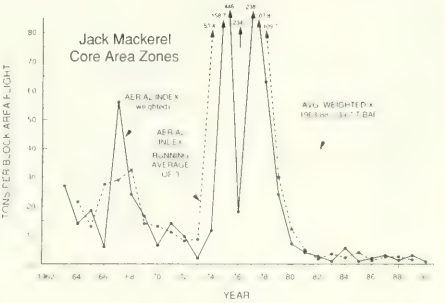

Figure 6

Abundance index levels in T/BAF for jack mackerel *Trachurus symmetricus* core area, night index, weighted $\bar{x}$, and running average (×3).

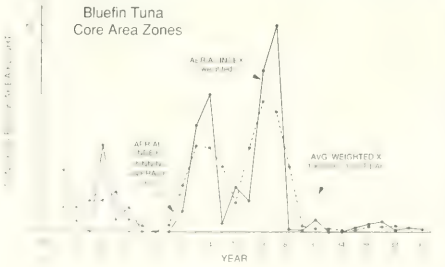

Figure 7

Abundance index levels in T/BAF for bluefish tuna *Thunnus thynnus* core area, night index, weighted $\bar{x}$, and running average (×3).

Interaction between species

To compare periods of high and low abundance of the six species, the logarithm of the moving weighted averages of core-area abundance indices (day or night, dependent upon which time the species was observed more frequently and in greater quantity) were plotted (Fig. 8). The dominant feature of Fig. 8 is the abundance index for the northern anchovy. High index levels of 200–500 T/BAF were recorded during 1962–82, a 21 yr period. The index declined sharply in 1983 and 1984, increasing since. The northern anchovy is the more stable species in terms of less annual percentage change in abundance than any of the other five species. During 1966 and 1967, jack mackerel, bluefin tuna, and Pacific bonito were at higher levels of abundance than those observed in the early 1970s. The Pacific sardine and chub mackerel resources were low in abundance by 1965, and declined to extremely low levels by 1970. The northern anchovy, jack mackerel, chub mackerel, and bluefin tuna increased in abundance in 1974–79. Exceptions were the Pacific bonito and sardine.

The very strong El Niño condition of 1982–83 (Quinn et al. 1987) had a significant effect on the distribution of coastal pelagic species (Fluharty 1984, Squire 1987). This period saw declines in abundance for all species, except Pacific bonito and chub mackerel. These two species showed significant declines in 1986–87. A rapid increase in Pacific sardine abundance was evident in 1984, immediately following the El Niño event and continuing into the late 1980s.

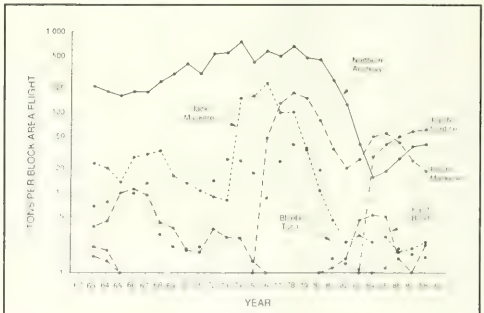

Figure 8

Comparison of core-area fluctuations in apparent abundance index levels for northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, chub mackerel *Scomber japonicus*, Pacific bonito *Sarda chiliensis*, jack mackerel *Trachurus symmetricus*, and bluefin tuna *Thunnus thynnus*. Data plotted on a semi-logarithmic scale, in weighted $\bar{x}$, T/BAF, by moving average (×3).

From inspection of core-area fluctuations (Fig. 8), it is difficult to draw any conclusions regarding interaction among most of the species included in this study. The annual abundance values that appear to be more closely related are those of the northern anchovy and bluefin tuna which were significantly correlated ($y=0.76$, $P<0.1$).

Pilot estimation of tonnage

Differences between pilots' ability to estimate school or group size are difficult to evaluate using the type of data recorded in flight logs. Computer recording of flight track and species tonnage observed did not include details of what portion of the block was searched, or where the species were sighted. Aerial spotters entering the block area (an 8×10 nm area) may have observed fish schools of the same species in two geographically different locations. Only the sum of the school sizes was coded.

The time of observation is probably the most critical factor in comparisons of pilot sightings because near-surface fish abundance may be highly variable over a short period of time. Therefore, unless pilots are searching the same area at the same time, different levels of abundance are likely to be observed.

Williams (1981) in surveys of pelagic fish resources off southeast Australia indicated that the professional fish spotters were extremely accurate in tonnage estimates of individual schools. In tests conducted by NMFS and CDF&G to determine northern anchovy school size using acoustic gear, a purse seiner and aerial spotter were used. The aerial spotter had a more accurate estimate of school tonnage than obtained from acoustic gear (P. Mardesich, Flying Fishermen, Inc., pers. commun. 1978).

MacCall (1975), using the NMFS computer database, investigated variation in anchovy abundance estimates (comparison of data collected during the same 10d period in 1973 and 1975) and found considerable differences among spotters. The differences were consistent for individual pilots for day and night observations. Variability in reported tonnage was large, but it could be reduced by long-term averaging. MacCall (1975) further suggested that corrections for pilots estimating efficiency be incorporated in calculations of the abundance index to avoid biasing the result toward the spotter with the highest tonnage. The accuracy of fish-spotter estimates of tonnage was approached statistically by Lo et al. (In press) using a delta-lognormal model. All aerial spotter data were used in this analysis. However, until spotter-pilot estimating efficiency is measured in field experiments, correction factors are unknown. It is possible that these differences between spotters may be due more to differences in numbers of schools seen than to differences in size estimates.

Comparison of aerial index to other abundance indices

The problem of variability among spotter pilots complicates comparisons; however, pilots are paid relative to the amount of tonnage caught. Therefore, the aerial spotter needs to have a reasonable estimate of school size to compare with the amount of fish caught by the seiner. The aerial spotter is continually obtaining "ground truth" from the purse-seine vessel relative to species composition and size of the school caught.

Since the decline of the Pacific sardine resource in 1984, considerable effort has been expended on surveys, using various techniques to collect apparent abundance data that could be modeled to produce an estimate of biomass. Acoustic, egg and larva, and aerial-spotter surveys have been conducted. Each survey measures a different component of the population and, therefore, comparisons of abundance estimates from different methods and models must be viewed with caution.

The aerial-spotter program measures apparent abundance of adults and subadults of epi-pelagic schooling fishes, and assumes that most adults in the population are available to the spotters at some time during the year. The aerial index is a direct calculation (T/BAF). It is a non-random type survey, but is not time-restricted.

The operational procedures used by aerial spotters affect the results. Although they do work closely with the fleet in locating and sometimes directing the setting of the purse seine, much of their time is spent searching large areas of the ocean for fishable resources. Many times, the aerial spotter will conduct flight operations in a general survey mode for the fleet, but does not work directly with the fleet. Even though aerial monitoring is conducted throughout the year, most observation effort is in the summer and early fall (49% of BAF during July, August, and September) when concentrations of commercial species are more common in the nearshore areas.

Quantitative apparent-abundance data derived from field surveys (egg and larvae, and acoustic) are statistically treated under various biological assumptions to ultimately obtain an estimate of biomass or tonnage: spawning biomass and total biomass in the case of egg and larva surveys (Lo 1985), and schooled biomass in the case of acoustic surveys (Mais 1974). Although some biomass estimates have been made for other species, such as the chub mackerel and Pacific

sardine, most biomass studies and modeling for the California region have involved the northern anchovy (Methot 1989).

Over the past 35 yr, studies by fishery biologists have produced a wide range of population estimates for a number of the pelagic species, in particular, the northern anchovy, Pacific sardine, and chub mackerel. The following describes the results of these and others in relation to aerial abundance indices.

Northern anchovy A review of the many abundance estimates for the northern anchovy over the years 1940–66 was given by Messersmith et al. (1969). For the early years of the aerial program, MacCall et al. (1974) compared anchovy biomass estimates from egg and larva surveys with the night aerial index, resulting in a correlation of +0.30 (1962–69). They also compared the aerial night index with the acoustic estimate (1966–72) producing a negative correlation (r=–0.47).

In a review of egg production of the northern anchovy central stock, Lo (1985) presented a correlation between various indices of anchovy spawning biomass. The biomass index from the aerial surveys had a high correlation (r=0.818) with egg production, and there was a similar correlation (r=0.807) between biomass egg production and acoustic surveys.

Correlation plots of normalized data (standard deviates; Snedecor 1959) were used to compare northern anchovy abundance data presented by Lo (1988) with aerial index values. The aerial index (day plus night) for the core area was compared with Lo's (1988) estimate of spawner biomass, determined from a combination of various estimates from the egg production method and the results of the 1969–85 sonar or acoustic surveys (Lo 1988), giving a correlation of r=0.61, df=14, P<0.05%. The aerial index was also compared with the estimate of schooled biomass based on results of acoustic surveys presented by Lo (1988), giving a correlation of r=0.51, df=13, P<0.05%.

MacCall & Prager (1988) presented anchovy larval-abundance indices for 1963–85. These indices, which are a measure of spawning population, were compared with the core-area aerial index for the same set of years. There was statistically significant correlation between the two indices (aerial/larva) (r=0.82, df=13, P<0.1).

Pacific sardine MacCall & Prager (1988) also reviewed the historical trend of sardine larval abundance, 1951–85. A comparison was made between their arithmetic scale of larval abundance (standard index) and the aerial index during the period 1963–85. Indications of a resurgence of the Pacific sardine resource began in 1978, and for the 1963–85 period MacCall & Prager's (1988) estimate of larval abundance correlates well with the aerial index (r=0.98, df=8, P<0.01).

Pacific bonito Pacific bonito, a species whose seasonal abundance off California is more closely associated with environmental conditions (El Niño effects) than the other species (Squire 1987), has not been subjected to detailed assessment. MacCall et al. (1974) used recreational partyboat CPUE data in yearly time-lag periods and compared this with the aerial index. The recreational partyboat fleet generally fishes nearshore and catches younger fish than the offshore commercial purse-seine fleet. The highest correlation (r=0.69) between the recreational fleet CPUE and the aerial index was for a 3 yr lag period (aerial index lags the recreational CPUE). No other independent estimates of Pacific bonito biomass are available for comparison.

Chub mackerel Assessment of the chub mackerel resource has used both standard population-dynamics techniques and methods that utilize egg and larva surveys. For comparison of changes in population over time, Squire (1983) plotted the trend of the aerial index against the spawning biomass index and the larva index of Smith & Richardson (1977). The limited data (1963–67) precluded any long-term comparison; however, all three indices showed a similar decrease. The aerial index was significantly correlated (P<0.05) with both spawning biomass (r=0.99) and the larva index (r=0.94).

The chub mackerel biomass declined to very low levels in the mid-1960s and remained very low until the mid-1970s. A sharp increase in biomass was noted starting in 1976. MacCall & Prager (1988) presented data on chub mackerel larval abundance through 1985. A correlation of the aerial index (core area) with the larva index for 1963–81 was statistically insignificant (r=0.205). A comparison made between the aerial index (core area) and estimated biomass of MacCall et al. (1985) for 1963–84 gave what would appear to be a good fit for the early years, but comparison of later years' estimates was not significant (r=0.26).

Jack mackerel Various indices of abundance for jack mackerel, including the aerial index, show that the resource tends to be highly variable in apparent abundance. Egg and larva surveys have shown the stock to be extremely widespread. Based on tagging data, Knaggs (1973) estimated between 700,000 and 1,500,000 t were available to the fishery in 1973. MacCall et al. (1974) stated that these estimates are in agreement with trends in aerial survey index (Squire

1972). MacCall & Prager (1988) presented graphics on a time-series of abundance indices for jack mackerel larva off southern California. They noted that the index did not correspond well with other larval indices that included samples from central California. An examination of the MacCall & Prager (1988) larva index vs. the aerial index indicated a poor correlation (r=0.16, not significant), particularly for the years 1977–78, a period of marked increase in jack mackerel abundance off southern California.

Bluefin tuna No biomass estimates are available for bluefin tuna in the northeast Pacific, which is part of a Pacific-wide resource. Young year-classes (1–3 yr) are common in the northeast Pacific with some catches of fish up to 6 yr of age (Bayliff 1980). CPUE estimates presented by Calkins (1982) of catch/boat-day (C/BD) for the U.S. purse-seine fishery operating off California and Baja California, Mexico for the years 1963–80 in the area north of 29° N lat. were compared with the aerial core-area mean index. Although both indices (C/BD and T/BAF) show a decline prior to 1980, the correlation was not significant (r=0.033). Calkins (1982) stated that "total catch may be the best indicator of bluefin abundance." Total catch (north of 29° N lat.) as given by Calkins (1982) was compared with the core-area index, and the correlation was again not significant (r=0.147).

Summary and conclusions

The aerial monitoring program has produced information on the trend of apparent abundance for six species of pelagic near-surface schooling species. The program in operation since 1962 utilizes information provided by commercial aerial fish spotters. Spotter pilots operate under strong incentive to estimate tonnage accurately, since their compensation is based on actual tonnage caught. The cost of the program is a small fraction of the cost of other field assessment methods currently used to develop apparent abundance data, such as egg and larva surveys and acoustic surveys.

Data are presented in a relatively simple and understandable index format of tons observed/block area searched (T/BAF). Annual indices (T/BAF) of apparent abundance are calculated for the major species of importance to the commercial purse-seine fleet operating off southern California and northwestern Baja California, Mexico.

All species have shown a fluctuating pattern of apparent abundance over the 29 yr survey period (1962–90). The northern anchovy is the dominant species observed, accounting for 89.7% of all tonnage observed; chub mackerel is second with 6.1%; followed by jack mackerel with 2.1%, and Pacific sardine, Pacific bonito, and bluefin tuna with 2.1%.

From inspection of abundance data, peak periods of higher abundance for four of the six species (chub mackerel, jack mackerel, northern anchovy, and bluefin tuna) occurred in 1977–79. Analysis indicated that species more closely related in abundance over time are the northern anchovy and bluefin tuna, both being at higher levels of abundance during 1972–80. A regression was calculated for 1963–88, giving a significant correlation (r=0.76, P<0.1).

A number of comparisons were made between estimates of biomass (spawning or total biomass) and the aerial abundance indices for the northern anchovy, Pacific sardine, and chub mackerel, and the apparent abundance of bluefin tuna based on CPUE data. There is a significant correlation with the aerial index, the anchovy total biomass estimate, and the historical egg-production index. Also, there was a slightly less but significant correlation with the acoustic survey estimates. The more significant correlations were found in comparing the aerial index with the northern anchovy larva index and the Pacific sardine larva index. For the chub mackerel, a species recognized as having a highly fluctuating record of abundance, the correlations during the early years (1963–66) were very good (aerial index vs. larva index and spawning biomass index); in later years, correlations between the larva index and the estimates of total biomass and the aerial index were not significant. There is a lack of good data relative to the abundance for other species of interest (Pacific bonito, jack mackerel, bluefin tuna) although some comparisons with the aerial data have been made for Pacific bonito, giving a reasonable correlation using a 3 yr lag period. Bluefin tuna C/BD (catch/boat-day) and total catch for the northwest Mexico–southern California fishery were compared with the aerial core index and gave no significant correlation.

Trends of aerial indices indicate that the pelagic resources studied can be described in a state of chaotic fluctuations (Jensen 1987) relative to apparent abundance. The fluctuating record indicates that even short-term predictions of abundance appear not to be feasible. Management must rely on near real-time estimates based on a measurement of a small fraction of the resource, and what is important is the development and use of more than one method or approach in evaluating population status. None of the survey results appear in complete agreement; however, utilizing several approaches to provide "triangles of agreement" (from a method used in navigation) can provide a consensus for management action.

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Differences in haplotype frequencies of mtDNA of the Spanish sardine *Sardinella aurita* between specimens from the eastern Gulf of Mexico and southern Brazil

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Abstract. – Analysis of restriction-site polymorphisms of mtDNA and Monte Carlo statistics were used to test the hypothesis that at least two genetic stocks of Spanish sardine *Sardinella aurita* are present in the eastern Gulf of Mexico, with one occurring at each of the two main fishery locations off Florida. Also included for comparison were specimens of Spanish sardine collected off southern Brazil. No significant heterogeneity of mtDNA haplotype frequencies was detected among specimens from the two locations within the Gulf of Mexico after analysis of 57 individuals (28 from Tampa Bay and 29 from the Florida Panhandle) using 9 informative restriction enzymes. However, highly-significant differences were observed between the specimens from the Gulf of Mexico and 16 specimens from southern Brazil. Based on counts of gill rakers of all specimens from both regions and the results of the mtDNA analysis, it is suggested that *Sardinella brasiliensis*, the Brazilian sardine, is conspecific with *S. aurita*, and that *S. aurita* is probably represented by genetically-identifiable populations in the western North and South Atlantic.

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Spanish sardine *Sardinella aurita* (Valenciennes) ranges in the western Atlantic from Cape Cod, throughout the Gulf of Mexico and Caribbean Sea, to southern Brazil (Whitehead 1973). It is also present in the Mediterranean Sea and in the eastern Atlantic off the African coast (Fisher 1978, Whitehead 1985). A second sardine species, *Sardinella brasiliensis* (Steindachner), reportedly occurs within the range of *S. aurita* between the Gulf of Mexico and southern Brazil (Whitehead 1973 and 1985, Johnson & Vaught 1986), but there have been no studies successful in fully differentiating the two species within the eastern Gulf of Mexico (Wilson & Alberdi 1991). There has traditionally been a small but important baitfish fishery for Spanish sardine off Florida with an annual landing of over 1500 t as recently as 1988. However, this fishery closed abruptly in 1989 after landings dropped sharply between 1988 and 1989. The closure was partly a response to uncertainty about the number of species or stocks being fished (Sutter & Mahmoudi 1992).

Management concerns about the sardine fishery in the eastern Gulf of Mexico involve the possibility of local stock depletion or collapse from increased fishing pressure at the two primary fishing areas in the eastern Gulf of Mexico, the Florida Panhandle and Tampa Bay. There is also concern over the possibility of overfishing one of the two species supposedly present. The first concern has arisen from the observation that Spanish sardines caught by the fisheries operating at these two locations appear to consistently differ morphometrically (Johnson & Vaught 1986), suggesting the possibility of separate genetic stocks or species. In response to these concerns, Wilson & Alberdi (1991) electrophoretically compared more than 300 specimens from the two areas at 41 presumptive genetic loci and found no important differences in allele frequencies, nor any fixed differences. They concluded that stock differences were only weakly indicated, and that no genetic evidence of two species of Spanish sardine in the eastern Gulf of Mexico had appeared.

Analysis of restriction-site polymorphisms of mitochondrial DNA (mtDNA) is generally regarded as offering a higher degree of resolution than protein electrophoresis in population genetic studies (e.g., Ferris & Berg 1987), and has recently become important in studies of potential fishery stocks. The most direct analytical approach is to compare the frequency distributions of composite mtDNA haplotypes among the sample populations, testing (x^2) whether the distributions are homogeneous and, therefore, indicative of stock mixing (Bentzen et al. 1989). However, the usually skewed distribution toward a common haplotype(s) coupled with the common occurrence of several rare haplotypes (Billington & Hebert 1991) in a population sample usually results in low sample numbers per cell in contingency tables, and tabulated values of x^2 cannot be used properly. This problem can be avoided, however, by using a Monte Carlo method of computing the exact x^2 expected from the observed haplotype frequencies among sample populations (Roff & Bentzen 1989, Bernatchez & Dodson 1990).

In this study we employ analysis of restriction-site polymorphisms of mtDNA and Monte Carlo statistics to test the hypothesis that the two main fisheries in the eastern Gulf of Mexico are comprised of at least two genetic stocks of *S. aurita*. We have included specimens of *S. aurita* collected off southern Brazil under an *a priori* expectation that stronger differences in mtDNA haplotype frequencies should exist between specimens from the Gulf of Mexico and southern Brazil. Considering the geographic proximity of our sample populations in the eastern Gulf of Mexico, and recognizing the fact that inadequate sampling of the mitochondrial genome (as evidenced by the number of restriction enzymes used) can bias the outcome in the direction of "no significant differences," inclusion of the Brazilian specimens allows us to objectively gauge the power of our methods to address the stated hypothesis.

Materials and methods

Specimens of *S. aurita* from the eastern Gulf of Mexico were obtained from the two main commercial fisheries along Florida's west coast, one near Tampa Bay and the other off the Panhandle. Individuals were collected fresh from both sites during the summer of 1989 (Fig. 1). Ripe ovaries were excised soon after capture and held on ice or in refrigerated buffer (MSB-Ca^{++} of Lansman et al. 1981) for up to 10d prior to purification of mtDNA; some ovaries from the Tampa Bay sample were stored frozen at –86 C until processing. The timing of specimen collections was structured to avoid resampling a single migrating school. Two samples were taken concurrently from Port St. Joe, Florida (n=10) and Destin, Florida (n=13) in May 1989, and a third sample was taken from Destin (n=6) in September 1989, for a total of 29 specimens (Fig. 1). In the Tampa Bay region a total of 28 individuals were taken during three collection times: February (n=12), May (n=10), and August (n=6) of 1989.

Whole fish specimens obtained from off Santos, Brazil were collected from the fishery and hand-carried frozen on dry ice to St. Petersburg, Florida within 2d and were stored at –86 C for several months without removing the ovaries. Because these specimens were

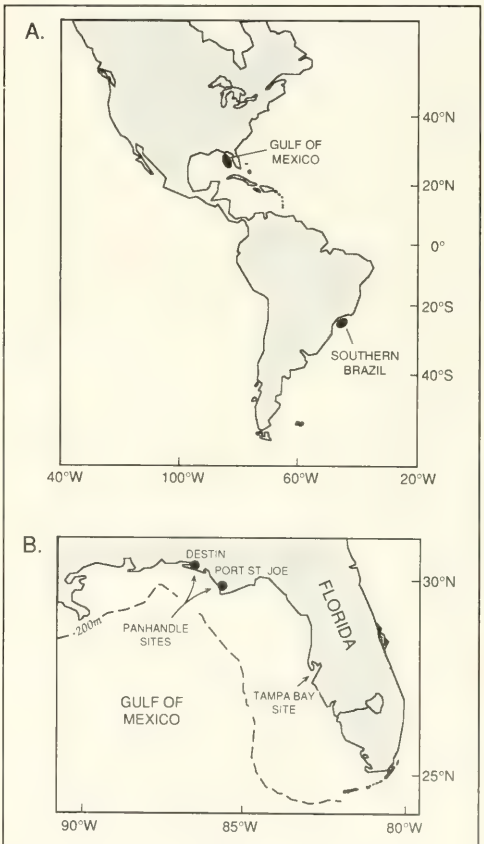

Figure 1

Collection sites of Spanish sardines *Sardinella aurita* in the eastern Gulf of Mexico and southern Brazil: **(A)** The two major sites, and **(B)** two area sites in the eastern Gulf of Mexico.

also used in the electrophoretic study of Wilson & Alberdi (1991), one thaw/refreeze cycle occurred prior to use in the present study. All specimens were identified to nominal species using the criteria of Whitehead (1973, 1985). That is, we counted the number of gill rakers on the lower limb of the first gill arch and related the count to standard length (SL), and we examined the condition (curled or flattened) of the anterior rakers of the lower limb of the first arch.

Mitochondrial DNA was purified from the ripe ovaries of the specimens taken from the Gulf of Mexico as in Wilson & Tringali (1990), except that the mtDNA collected after density-gradient ultracentrifugation was extracted in n-butanol which was not saturated with NaCl. This removed most of the salts, allowing greater precision over the molar concentration of the DNA-containing solution during the ethanol precipitation. The lower yield of mtDNA caused by thawing and refreezing of the Brazilian specimens necessitated use of a modification of the Chapman & Powers (1984) method of extraction (Tringali 1991).

Restriction digests were carried out as specified by the manufacturers using the following enzymes: *Apa*-I, *Bam*H-I, *Dra*-I, *Eco*R-I, *Hin*d-III, *Pst*-I, *Pvu*-II, *Sac*-I, *Xba*-I, and *Xho*-I. Fragments were separated by horizontal agarose gel electrophoresis and visualized in most cases using the gel-incorporated Hoechst 33258 (CalBiochem #SR5A03-0388) fluorochrome dye as in Deflaun & Paul (1986). However, some poor yields of mtDNA during purification made visualization of the smaller restriction fragments difficult using the fluorochrome, thus requiring application of an mtDNA hybridization probe to southern blots of the agarose gels (Tringali 1991). The non-radioactive hybridization probe was made from cesium-purified mtDNA of *S. aurita* using a commercial kit (Genius Kit of Boehringer Mannheim, Cat. #1093657). Hybridization and immunological detection of the probe was performed as specified by the manufacturer with the following modifications. The concentration of the blocking reagent in the prehybridization and hybridization solutions was doubled to 1.0% weight/volume to reduce background coloring of the hybridization filter (Zeta-Probe). The prehybridization period was extended to a minimum of 2h and the volume of the probe-containing hybridization solution was increased to 10 m L/100 cm^2 of filter. The ELISA reaction period was increased to 2 h. Under these modifications, the mtDNA restriction fragments were usually visible on the filter ~15 min into the color reaction.

Molecular weights (in base pairs) of the restriction fragments were estimated by the global form of the reciprocal method as described in Elder & Southern (1987). Restriction-fragment length polymorphisms (RFLPs) were expressed as two data types: restriction-site data and composite mtDNA haplotypes. The restriction-site composition of each individual was inferred from fragment profiles and intraspecific sequence diversity (Nei & Miller 1990) was calculated using the RESTSITE v1.2 algorithm. Composite mtDNA haplotypes were constructed for each individual from their restriction profiles with haplotypes grouped by sample location and time of collection. The frequency distribution of mtDNA haplotypes was tested for heterogeneity, with respect to location and time, by the log-likelihood G-test for independence (Sokal & Rohlf 1981). G-tests were also performed on selected samples following generation of 100 randomized data sets from the observed data, using the Monte Carlo technique described by Roff & Bentzen (1989) where the probability, P, of obtaining a randomized G_H value greater than the original observed value is given by

$$P = n / N_r \quad (1)$$

where n equals the number of outcomes in which the randomized G_H value is greater than the actual G_H value, and N_r represents the number of randomizations performed. The standard error of P was taken as

$$[P(1 - P)/N_r]^{1/2}. \quad (2)$$

The frequency of the most common haplotype was tested, after arcsine square-root transformation (Freeman & Tukey 1950), using the "V" statistic (Desalle et al. 1987) for heterogeneity between sampling locations.

Results

Counts of gill rakers identified 72 of 73 sample specimens as *S. aurita*; one specimen from Brazil had gill-raker counts expected for *S. brasiliensis*. Counts were lowest for the Panhandle specimens while specimens from Tampa Bay and southern Brazil were the most similar, having higher counts (Table 1). Specimens from the Florida Panhandle were of larger average size than those from Tampa Bay and southern Brazil, which were more similar in size (Table 1). A one-way analysis of variance revealed significant heterogeneity ($P<0.05$) in gill-raker counts between the specimens taken from the Panhandle and Tampa Bay, but not between those taken from Tampa Bay and southern Brazil. One Brazilian specimen had a gill-raker count of 154 at 150 mm SL, nearly identical to that reported for the lectotype of *S. brasiliensis* (155 at 148.3 mm SL; Whitehead 1973). However, we could detect no differences in the appearance of the anterior rakers (curled vs. flattened) for this or other specimens. The overall appearance of the rakers of all specimens most closely resembled Whitehead's (1985) diagrammatic drawing

Table 1

Data for Spanish sardines *Sardinella aurita* used in mtDNA analysis.

Location	Number counted	Size range[1] (mmSL)	gill-raker count Mean[2]	gill-raker count Range
Port St. Joe (Panhandle)	10	162–189	113±11SD	102–127
Destin (Panhandle)	19	159–189	114±9	99–128
Tampa Bay	28	149–171	134±7	121–145
Santos, Brazil	16	149–181	132±9	122–154

[1] Mean length of pooled specimens from the Panhandle is significantly larger than that of specimens from the other two regions (ANOVA, $P<0.05$).

[2] Mean number of gill rakers of pooled specimens from the Panhandle is significantly lower than that of specimens from the other two regions (ANOVA, $P<0.05$).

of *S. brasiliensis*, curling anteriorly downward. However, use of this character was extremely problematic for us because, other than the drawing, we found no published taxonomic account of the discovery of this character, no photographic evidence nor written description detailing the character, nor reference of this character to [any] catalogued or type material.

The combination of mtDNA purification and visualization techniques used here provided well-resolved digestion patterns that could be consistently and unambiguously scored for all individuals. Of the 10 restriction endonucleases used, only *Bam*H-I was not informative. This enzyme had but one restriction site in all samples and was used only in probe construction to linearize template mtDNA prior to labeling. Polymorphic digestion patterns occurred for the remaining nine enzymes, with *Pst*-I and *Pvu*-II highly variable (Table 2). The mean mtDNA genome size, calculated from the sums of all digestion patterns, was 16,304 base pairs (bp) ± 71 bp (SD). No size variation was detected between specimens or within the mtDNAs of individual specimens.

The nine informative enzymes sampled 52 unique restriction sites over all individuals (Table 3) with a mean of 43 sites per individual. All RFLPs were consistent with the assumption of a single nucleotide substitution between variant digestion patterns. Intraspecific sequence diversity (Nei & Miller 1990) over all individuals was 0.00525±0.00204 (bootstrapped SE) substitutions per nucleotide, a value consistent among all three sampling locations ($\bar{x}$=0.00509±0.00054, range 0.00452–0.00561). Twenty-four composite mtDNA haplotypes were generated from polymorphic restriction-fragment profiles of the 73 completely characterized Spanish sardines (Table 4). The composite mtDNA haplotype (BAABAAAAA) of the one putative *S. brasiliensis* specimen with a gill raker count close to the lectotype's (Whitehead 1970, 1973) was identical to that of another Brazilian specimen having the low gill raker count indicative of *S. aurita* (126 at 169 mm SL), as well as to that of seven specimens from the Gulf of Mexico (Table 4). The mtDNA haplotype most common in the Gulf of Mexico, AAAAAAAAA, occurred in very low frequency among the Brazilian specimens. The frequency of this haplotype was significantly different between specimens of the Gulf of Mexico and Brazil (V=10.90, $P<0.001$), but not among specimens from the different regions within the Gulf of Mexico (Table 5).

Ten composite haplotypes were unique to the Panhandle region, four to the Tampa Bay region, and five to Brazil. Four were observed in all three locations. G-tests of mtDNA haplotype frequencies for temporal and geographical heterogeneity among specimens from within the Gulf of Mexico did not allow rejection of the null hypothesis of population homogeneity ($P>0.05$). Pooling the Gulf specimens by location and testing for heterogeneity between locations using Monte Carlo statistics (100 randomizations) generated 35 G_H values exceeding the initial value of 25.774, again indicating that the null hypothesis of homogeneity for specimens taken within the Gulf of Mexico cannot be rejected ($P>0.35$, 2SE=0.09). Pooling all Gulf specimens and testing against the Brazilian specimens using Monte Carlo statistics resulted in a G_H value of 44.282 which was not exceeded by any of the 100 randomizations, indicating significant heterogeneity between specimens from those locations ($P<0.01$).

Discussion

Our results indicate an evident lack of genetic stock structuring between the commercially-fished populations of Spanish sardine in the eastern Gulf of Mexico, even though there is a significant difference in the average number of gill rakers between locations, in addition to the morphometric differences reported by Johnson & Vaught (1986). This significant variation in gill-raker counts relative to SL appears to confirm Whitehead's (1973) reference to two rates of increase in the number of gill rakers with increasing standard length among Spanish sardines of the western Atlantic, although the lowest counts (Panhandle) were lower than those Whitehead (1973) mentioned. Whitehead (1973) thought this variation in gill-raker counts indicative of the presence of two valid species of Spanish sardines in the western Atlantic, but our mtDNA analysis does not support his suggestion.

Table 2

Approximate sizes (base pairs) of restriction fragments from mtDNA of *Sardinella aurita*. Letters designate genotypes observed with each enzyme. "A" genotype was the most common for each enzyme.

Apa-I		*Bam*H-I	*Dra*-I		*Eco*R-I		*Hin*d-III		
A	B	A	A	B	A	B	A	B	C
6457	6457	16356	10233	8434	5621	5621	4169	3342	6607
7405	7405		5623	5623	4069	4069	3342	3296	4169
1948	1948		438	1798	3436	3436	3296	2661	2661
360	460			438	1318	1318	2661	2251	2104
107					665	1147	2104	2104	436
					620	665	436	1929	331
					525		331	436	
								331	
16277	16270	16356	16294	16293	16254	16256	16339	16350	16308

Pst-I							*Xho*-I		
A	B	C	D	E	F	G	A	B	C
4880	7100	7100	4360	4880	8184	4880	10965	9593	16274
4360	4360	4880	4200	4360	4880	4360	5309	5309	
3850	4200	4360	3850	3800	3150	3850		1372	
3150	564		3150	3000		2350			
			564	150		750			
16249	16224	16340	16124	16190	16214	16190	16274	16274	16274

Pvu-II								*Sac*-I	
A	B	C	D	E	F	G	H	A	B
6461	6461	10133	10133	6461	6461	6461	10753	7786	15230
4265	3672	2238	2238	3672	4770	3672	2238	7444	912
2238	2238	1779	1779	2238	2238	1878	1778	912	
1778	1778	1188	912	1779	1779	1778	912		
912	1188	912	690	912	912	1188	505		
505	912	230	505	690	230	912	230		
230	230		230	505		360			
				230		230			
16389	16479	16480	16487	16487	16390	16479	16416	16142	16142

Xba-I	
A	B
8317	6905
4809	4809
	2248
2248	1402
685	685
	335
16394	16384

The intraspecific sequence variability of mtDNA of *S. aurita* is comparable to that observed in most other marine fishes. With a mean sequence divergence of about p=0.51 (Nei & Li 1979), the mtDNAs of Spanish sardines of the Gulf of Mexico fall within the range of mean values observed among other clupeids, i.e., between 0.37% for shad (Bentzen et al. 1989) and 2.4% for menhaden (Avise et al. 1989). In both shad (Roff & Bentzen 1989) and menhaden (Bowen & Avise 1990), population-level mtDNA variability was observed

Table 3

Site matrices inferred from RFLPs of *Sardinella aurita*. Letters denote restriction patterns. Column numbers are the restriction sites observed over all individuals for the given enzyme. Inside the matrices: 1=site presence, 0=site absence.

	Pst-I							*Xba*-I						*Hin*d-III							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
A	1	0	1	1	1	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1
B	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
C	1	0	1	1	0	0	0							1	0	1	0	1	1	1	1
D	1	1	1	1	1	0	0														
E	1	0	1	1	1	0	1														
F	1	0	1	0	1	0	0														
G	1	0	1	1	1	1	0														

	Pvu-II									*Dra*-I				*Apa*-I				
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
A	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1
B	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0
C	1	0	1	0	1	1	1	1	0									
D	1	0	1	1	1	1	1	1	0									
E	1	1	1	1	1	1	1	1	0									
F	1	1	0	0	1	1	1	1	0									
G	1	1	1	0	1	1	1	1	1									
H	1	0	0	1	1	1	1	1	0									

	*Eco*R-I							*Xho*-I			*Sac*-I		
	40	41	42	43	44	45	46	47	48	49	50	51	52
A	1	1	1	1	1	1	1	1	0	1	1	1	1
B	1	1	1	1	1	0	1	1	1	1	1	0	1
C								1	0	0			

within the geographic regions sampled. Thus, the evident lack of significant heterogeneity in mtDNA haplotype frequencies among the Gulf specimens of *S. aurita* is probably not due to an inadequate level of mtDNA genome sampling relative to the sequence variability present.

Accepting that the mtDNA variability among sample locations of *S. aurita* was sufficiently characterized, at least two possibilities could account for the observed genetic homogeneity between our sample locations in eastern Gulf of Mexico. This lack of genetic structuring is the result of recent or ongoing genetic exchange between the sampled locations, or there may have been insufficient time for discrete Gulf populations, if they do exist, to diverge through mtDNA lineage sorting. The first explanation seems the more likely one, considering the life history of the species. *S. aurita* is known to be highly migratory (Hildebrand 1963, Simpson & Gonzalez 1967) and to spawn repeatedly throughout much of the year (Grall 1984). Although the pattern of adult migration of *S. aurita* in the eastern Gulf is still poorly understood, spawning occurs continuously between the Panhandle and Tampa Bay with no apparent geographic partitioning in either the distribution or abundance of eggs or larvae (Houde 1976). There are no known physical barriers to dispersal or migration in this region.

Significant geographic variation in mtDNA haplotype frequencies does exist between Spanish sardines in the eastern Gulf of Mexico and waters off southern Brazil, based upon the results of goodness-of-fit testing. This variation is due to two related factors. One is that the haplotype most common among the pooled specimens from the eastern Gulf of Mexico, AAAAAAAAA, possessed by 46% of the specimens, has a much lower occurrence (6%) among the specimens from southern Brazil. The other is the difference in the distribution of the *Pst*-I digestion pattern. Whereas 5 of 16 (31%) of the Brazilian specimens possessed the G-type pattern (Table 2), this pattern was absent in the Gulf specimens (n=57). Relative to the common A-type pattern of *Pst*-I present among the Gulf specimens, this G-type pattern represents a site gain at *Pst*-I.

Table 4

Frequency distribution of the 24 composite haplotypes from 73 *Sardinella aurita* from the western Atlantic. Restriction enzymes are in the following order: *Pst*-I, *Xba*-I, *Hind*-III, *Pvu*-II, *Dra*-I, *Apa*-I, *Eco*R-I, *Xho*-I, and *Sac*-I. Frequency distribution of pooled haplotypes from the Gulf of Mexico differ from the Brazilian at $P<0.01$ ($G_H=44.282$).

Haplotype number	Composite digestion profile	Panhandle Florida	Tampa Bay Florida	Santos Brazil
1	AAAAAAAAA	14	12	1
2	BAABAAAAA	1	6	2*
3	AAADABAAA	1		
4	AABAAAAAA	1		
5	BAACBAABA	1		
6	BBABAAAAA	1		
7	BAACAAAAA	2	1	
8	CAAAAAAAA	1		
9	DAAAAABAA	1		
10	BAAFAAAAA	1		
11	CAABAAAAA	1	4	3
12	AAAAAAACA	1		
13	AAAEAAAAA	1	1	1
14	EAAAAAABA	1		
15	AAAEABBAA	1		
16	BAABAAAAB		1	
17	FAAAAAAAA		1	
18	BAAGAAAAA		1	
19	AAAFAAAAA		1	
20	AAAHAAAAA			2
21	GACAAAAAA			2
22	GAAAAAAAA			3
23	BAAAAAAAA			1
24	AAAAABAAA			1
		29	28	16

*Including specimen identified as *S. brasiliensis* by gill-raker count.

Table 5

Tests for temporal and geographic heterogeneity of *Sardinella aurita* mtDNA haplotypes. G_H values were generated by comparing the complete distribution of mtDNA haplotypes for each group. "V" statistics were calculated by comparing the frequency of angular-transformed Haplotype 1 between regions.

Sample	G_H	df	V	df
Tampa Bay vs. Panhandle	24.278	17	0.01	1
Tampa Bay vs. Brazil	29.302*	12	9.68*	1
Panhandle vs. Brazil	39.386*	19	11.49**	1
Pooled Gulf of Mexico vs. Brazil	44.282*	23	10.90**	1

* $P<0.05$, ** $P<0.001$ (from tabulated critical values of the x^2 distribution).

We interpret the significant heterogeneity in haplotype frequencies between specimens from the eastern Gulf of Mexico and southern Brazil as genetic stock differences between Spanish sardines of the western North and South Atlantic, rather than as species differences as, for example, between *S. aurita* and *S. brasiliensis*. The one specimen of this study referable to *S. brasiliensis*, with a gill-raker count of 154 at 150 mmSL, came from southern Brazil, but it had one of the mtDNA composite haplotypes (haplotype 2; Table 4) present among specimens from the eastern Gulf of Mexico. All other specimens from both Gulf and Brazilian waters possessed the lower gill-raker counts typical of *S. aurita*.

This interpretation also agrees with results of the electrophoretic study of Wilson & Alberdi (1991). After comparing 350 specimens from the eastern Gulf of Mexico with 41 specimens of Spanish sardine from off southern Brazil at 36 presumptive gene loci, they found no genetic evidence of more than one species of Spanish sardine in those two areas. That is, there were no fixed allelic differences that would suggest the presence of fully segregated gene pools, as in two species. Neither in the present study nor in that of Wilson & Alberdi (1991), which used the same Brazilian specimens as here, was our nominal *S. brasiliensis* distinguishable from *S. aurita* by electrophoretic genotype or mtDNA haplotype.

We think it likely that *S. brasiliensis* is conspecific with *S. aurita*. Whitehead (1970) removed *S. brasiliensis* from the synonymy of *S. aurita* on the observation that the syntypes of *S. brasiliensis* from off Brazil had both high and low gill-raker counts at similar lengths. That is, he concluded that the syntypes with low gill-raker counts were *S. aurita* and that the others with high gill-raker counts were *S. brasiliensis* of Steindachner. Whitehead (1973) again proposed the specificity of *S. brasiliensis* on this character based on his review of published data on gill-raker counts of western Atlantic *Sardinella*, but he did not report data from any additional specimens. Whitehead (1985) proposed that *S. brasiliensis* might be distinguished from *S. aurita* based on the shape of the gill rakers forming the branchial basket, i.e., flattened in *S. aurita* vs. curled in *S. brasiliensis*, but he did not specifically connect this character to catalogued specimens which he examined. No mention was made of this character in his prior discussion of the syntypes (Whitehead 1970).

To our knowledge, no thorough quantitative study of variation in gill-raker counts with SL among Brazilian sardines has been published. Montero & Perez

(1981) conducted a protein electrophoretic comparison at 24 presumptive loci of Brazilian *Sardinella* which had been first identified as either *S. brasiliensis* or *S. aurita* by high or low gill-raker counts, respectively. They reported no electrophoretic differences between the two putative species, which is consistent with our finding of significant variation in gill-raker counts between specimens from the Florida Panhandle and Tampa Bay in the apparent absence of any genetic differences (Table 1). Thus, the higher gill-raker counts which supposedly distinguish *S. brasiliensis* from *S. aurita* are probably due to non-genetic causes, and are of no greater taxonomic importance than the intraspecific variation in gill-raker counts observed between *S. aurita* inhabiting the Panhandle and Tampa Bay locations of the eastern Gulf of Mexico (Table 1). Until the present classification of Western Atlantic *Sardinella* is supported by a thorough study of variation in the characters on which it is based, the validity of *S. brasiliensis* as a species is in question.

Given the non-reticulate nature of mtDNA transmission, it is not difficult to understand intraspecific divergence when there is a mechanism between populations affecting the balance between gene flow and genetic drift. There are a number of potential barriers to gene flow within the trans-equatorial range of *S. aurita*, including diverging oceanic currents (e.g., the North Equatorial current) and the major river plume of the Orinoco which can extend far out into the Caribbean. Even without discrete physical barriers, the stochastic process of mtDNA lineage survival or extinction might in itself be enough to alter haplotype frequencies in this continuously-distributed species if the effective gene flow is low relative to the sizes of the populations or their geographic ranges (Neigel & Avise 1986). However, the mtDNA variability among *S. aurita* might be a product of differential selective forces because the species is distributed over so great a latitudinal (environmental) gradient. For the Spanish sardine of the western Atlantic, there are not yet enough data to choose between the alternative hypotheses of drift vs. selection in accounting for the evident genetic structuring.

To our knowledge, this report represents the first substantiated case of a holopelagic teleost with a supposedly continuous distribution between sample regions (Gulf of Mexico to southern Brazil) exhibiting significant heterogeneity in mtDNA haplotype frequencies. Whereas other studies (e.g., Graves & Dizon 1989) have compared sample populations of holopelagic fishes removed by great longitudinal distances, or on opposite sides of land masses (Ovenden et al. 1989), ours is the first to compare specimens at near-opposite ends of a trans-equatorial distribution spanning many degrees of latitude (30°N to 26°S). Not only do these results further confirm the potential usefulness of mtDNA in studies of hypothesized fishery stocks, but also suggest the need for additional studies on fishes having similar distributions.

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Estimated drift gillnet selectivity for albacore *Thunnus alalunga*

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Drift gillnet (DGN) fisheries, some directed toward albacore *Thunnus alalunga* and some toward other species, have operated in the north and south Pacific Ocean. These fisheries, some of which had their beginnings decades ago, expanded in the early 1980s and exerted a substantial, but as yet unknown, mortality on Pacific albacore populations. Knowledge of the selectivity of DGNs is useful for applying complex population-dynamics techniques to the albacore population.

Several DGN experimental surveys conducted in the north and south Pacific Ocean have produced data on albacore distribution and gear selectivity. In 1984–85 the Southwest Fisheries Science Center of the National Marine Fisheries Service (NMFS) undertook an experiment to quantify DGN mesh-size selectivity for albacore. The experiment produced size-selectivity data for a single mesh size used in the U.S. DGN commercial fishery for albacore (184 mm; all mesh sizes referred to are stretch mesh measurements), in the eastern North Pacific Ocean. Other experiments designed to sample albacore were conducted by the Japan Marine Fishery Resource Center in 1980 (JAMARC 1983), 1982 (JAMARC 1985), and 1983 (JAMARC 1986). These experiments used other mesh sizes which produced complimentary data used in this study. The objective of this analysis was to quantify drift gillnet mesh-size selectivity for albacore, using existing data collected from various experiments and surveys in the Pacific Ocean.

Methods

Various experiments providing data have been conducted independently at different times and in different areas (Fig. 1). Consequently, some assumptions had to be made concerning comparability of nets used and availability and vulnerability of fish sizes to be sampled. However, there was enough information to provide insights into net selectivity for albacore. The nets used in all the experiments were similar to typical Japanese commercial drift nets. All nets had similar mesh-hanging ratios, twine/mesh-size ratios, and were of multifilament construction (Table 1). These are the most important factors affecting the selectivity curve for a given mesh size (Hamley 1975).

Detailed descriptions for the JAMARC experiments, including set locations, timing, mesh size placement, etc, are contained in the JAMARC references. These experiments were designed to obtain information on resource distribution and catch rates for possible future commercial fisheries. In brief, the JAMARC North Pacific experiment was a 1yr survey beginning in the spring of 1980 (Fig. 1). It targeted albacore using nets with mesh sizes of 130–250mm. The JAMARC 1982 and 1983 experiments in the South Pacific were conducted in the area shown in Fig. 1 and targeted all tuna-like species, using 180 mm mesh nets in 1982, and 118 mm and 160–180 mm mesh nets in 1983.

The NMFS experiment targeted albacore. A total of 27 night sets was made: 12 sets in waters south of Point Conception and within 300 mi of shore; 7 sets in the vicinity of the Guide Seamount south of the Farallon Islands; and 8 sets approximately 1000 mi west of Oregon near 142°W long. and 45°N lat. (Fig. 1). All sets used 184 mm mesh nets.

In all the experiments using mesh sizes of >130 mm, the amount of gear fished during each set ranged from 2760 m to 10,800 m, and the number of sets ranged from 11 to 176 (Table 1). Nets in each experiment were deployed and retrieved as in typical commercial operations. Nets were deployed at dusk, and retrieval began at first light often extending into midmorning. Soak times were ~10–16 h/set.

Data collected

Data published by JAMARC are limited to fork length (FL) frequencies by mesh size by set. The NMFS data include fork length-frequencies, maximum or largest body girth, and opercular girths for each fish, and notation on the mode of capture for each fish (tangled, wedged, or gilled). Fish were described as wedged or gilled when inserted into a mesh so that the entire perimeter of the mesh held the fish. This occurred at locations on the body from the snout to the point of maximum body girth. Fish were described as tangled when snared or tangled by fins or tail. Length-frequencies for U.S. troll-caught fish from the same time and areas are available for

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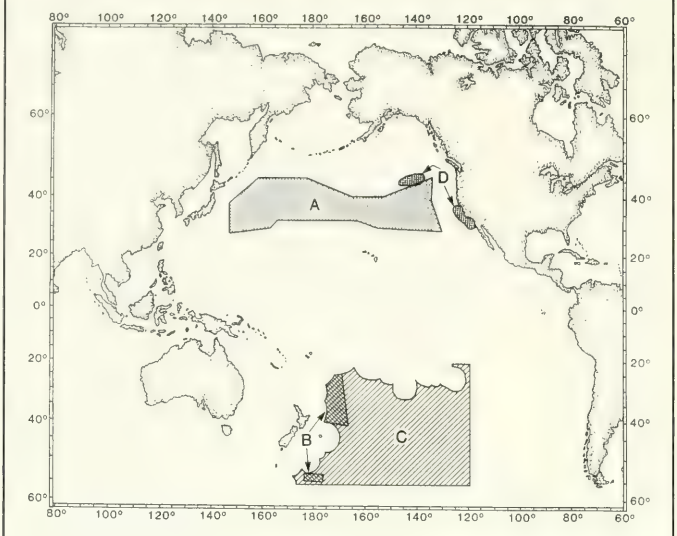

Figure 1

Areas sampled for albacore *Thunnus alalunga* by drift gillnets. **(A)** JAMARC 1980 survey (JAMARC 1983); **(B)** JAMARC 1982 survey (JAMARC 1985); **(C)** JAMARC 1983 survey (JAMARC 1986); **(D)** NMFS 1985 experiment.

Table 1

Characteristics of drift gillnets used, amount of gear fished, and alalunga caught for selected stretch mesh sizes.

Survey	Mesh size	Twine size (dinier/ strand)	Net material	Hang-in-ratio (% stretch mesh Distance/ hanging)	No. set
JAMARC 1980	130	210/21	Nylon	56.1	
(JAMARC 1983)	150	210/24	Nylon	56.1	
North Pacific	160	210/27	Nylon	56.1	
	170	210/30	Nylon	55.5	
	180	210/33	Nylon	56.1	
	200	210/36	Nylon	56.1	
	All				178
JAMARC 1982 (JAMARC 1985) South Pacific	180	210/30	Nylon	55.3	38
JAMARC 1983 (JAMARC 1986) South Pacific	118	210/10	Nylon		11
NMFS 1985 North Pacific	184	210/18	Polyester	50.0	27

comparison. Sample sizes of albacore caught by mesh size for each experiment, as well as the quantity of gear fished, are shown in Table 1.

Results

JAMARC 1980 data

Gear selectivity can only be estimated because there is no information on the actual size structure of the North Pacific albacore population (Hamley 1975). Data from several mesh sizes fished simultaneously and assumptions about shape, variance, and efficiency of the selectivity curves are required. The JAMARC 1980 experiment provided the only published dataset containing this information. Length-frequencies obtained in the 1980 experiment for mesh sizes 130, 150, 160, 170, 180, and 200 mm are shown in Fig. 2 (A–F). In all these mesh sizes, albacore captured had size modes at 53, 62, and 78 cmFL.

Two options are available for calculating an indirect selectivity curve: (1) Fitting a predetermined distribution function to data, using a method similar to that of Ishida (1962); or (2) estimating the selectivity of different meshes to one common size-class (mode) of fish and extrapolating to other mesh sizes (Regier & Robson 1966). Lack of an objective mathematical function in determining the shape of the selectivity curve in the first method, and the need for fitting the selectivity curve "by eye," required that a combination approach was employed.

A basic assumption of gillnet selectivity analysis is that selectivity is the same for those combinations of length interval L(i) and mesh size M(j) where the ratios of L(i)/M(j) are equal (Regier

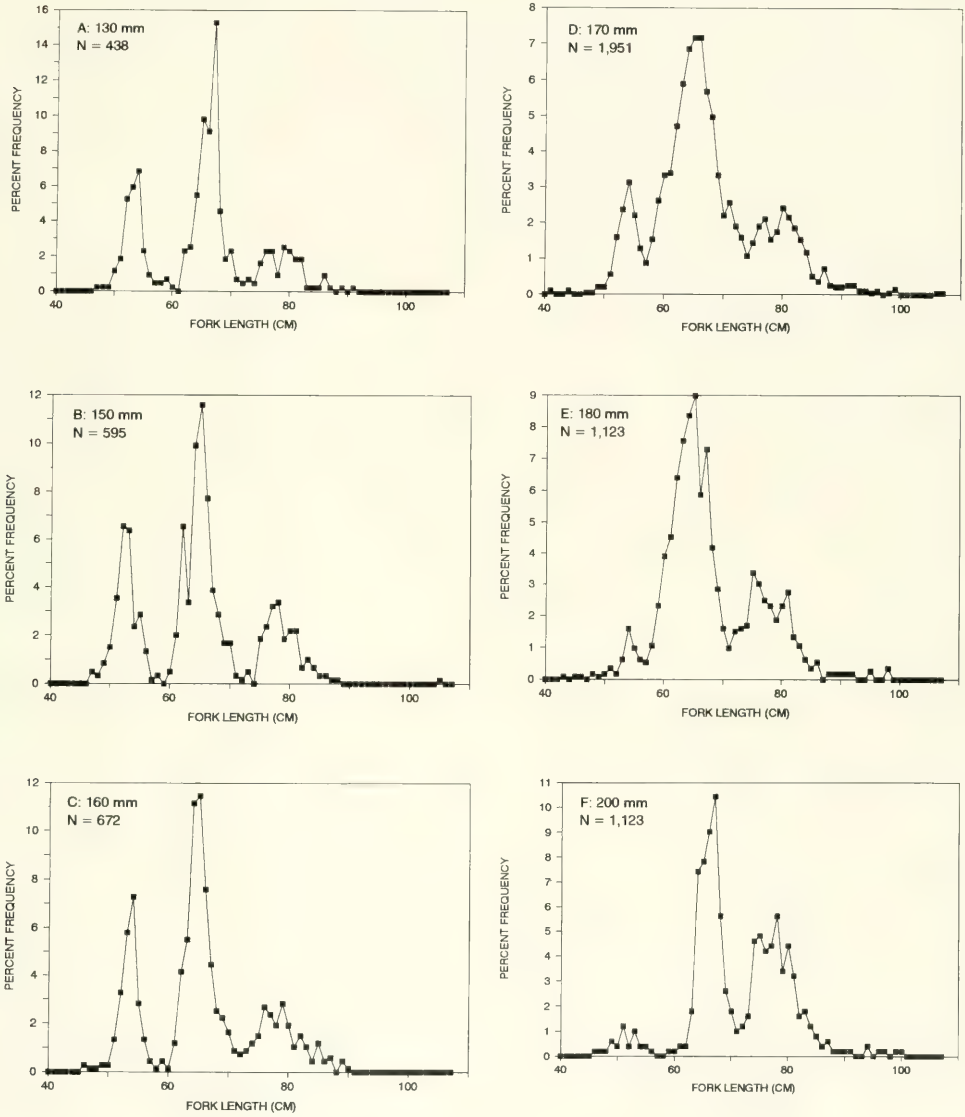

Figure 2

Percent frequency-of-occurrence of albacore *Thunnus alalunga* by fork-length interval by stretch-mesh size. Data from the 1980 JAMARC survey (JAMARC 1983). **(A)** 130mm mesh; **(B)** 150mm mesh; **(C)** 160mm mesh; **(D)** 170mm mesh; **(E)** 180mm mesh; **(F)** 200mm mesh.

& Robson 1966). This assumes that the length:girth ratio is the same for all fish. Each fork-length interval was divided by the appropriate mesh size of capture, and then multiplied by the appropriate observed frequency. This produced "generic" size-frequencies by mesh size. Each resulting size-frequency interval, by mesh size, was normalized to the greatest frequency. The resulting frequencies, one for each mesh size, were then scaled to an assumed 100% efficiency at the peak frequency sampled (the mid-60 cm mode); thus, differential sample sizes by mesh are taken into account. If all mesh sizes have the same selectivity curve, and no sampling variance, they would all be the same.

Rather than using the method of Ishida to describe a common selectivity curve (Regier & Robson 1966), the "mean" shape of the selectivity curve was estimated from the selectivity of the different mesh sizes for the largest (78 cmFL) and smallest (53 cmFL) modes captured by all mesh sizes. The curve obtained for the 53 cm mode described the left or ascending limb of the selectivity curve, and the curve for the 78 cm mode described the right or descending limb. Lengths between these two limbs were assumed to be sampled at 100%. This included some lengths with very low percent-frequencies (i.e., we assumed few fish were available) as well as the size mode near 62 cm. There was no assumption that the left and right limbs have the same shape.

For the 78 cm mode, the cumulative percent-frequency of capture vs. length of fish caught for all mesh sizes are shown in Fig. 3. When plotted on normal probability scales, cumulative percent-frequencies

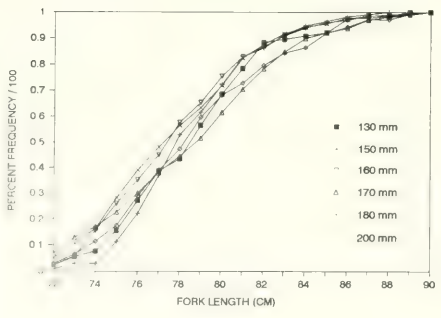

Figure 3

Cumulative percent frequency-of-occurrence by fork-length interval for 130 mm, 150 mm, 160 mm, 170 mm, 180 mm, and 200 mm stretch mesh sizes for the 78 cmFL mode of albacore *Thunnus alalunga* sampled in the 1980 JAMARC survey (JAMARC 1983).

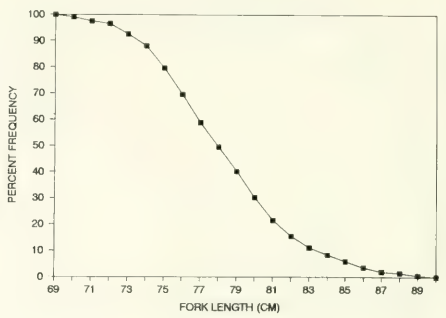

Figure 4

Mean selectivity-curve right limb for albacore *Thunnus alalunga* from the 78 cmFL mode sampled in the 1980 JAMARC survey (JAMARC 1983).

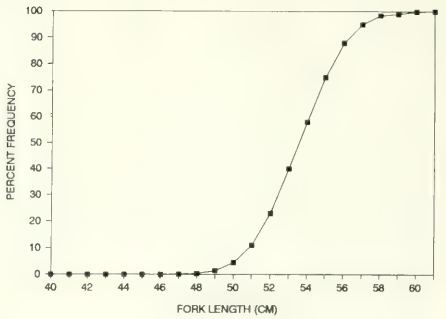

Figure 5

Mean selectivity-curve left limb for albacore *Thunnus alalunga* from the 53 cmFL mode sampled in the 1980 JAMARC survey (JAMARC 1983).

formed straight lines with virtually the same slopes. An average cumulative percent-frequency (subtracted from 100) provided the shape of the right limb (Fig. 4). This introduced the assumption of a constant variance and normal distribution (Hamley 1975). The same procedure provided the left limb of the selectivity curve which increased more rapidly or had a greater slope (Fig. 5).

These two limbs must now be placed appropriately on the X axis for each mesh size. This is accomplished separately for each limb by mesh size. The sampling efficiency at 53.5 cmFL for each mesh size was estimated by linear regression. The observed maximum

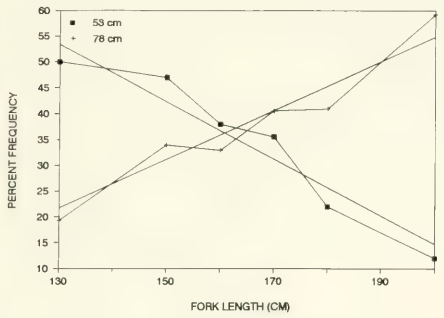

Figure 6

Linear regressions of observed maximum percent sampling efficiency at 53 cm and 78 cmFL against stretch-mesh size for albacore Thunnus alalunga.

Table 2

Estimated percent sampling efficiency for albacore *Thunnus alalunga* at fork lengths of 53 cm and 78 cm for various stretch mesh sizes.

Mesh size (mm)	Fork length (% efficiency)	
	53cm	78cm
130	53.3	21.7
150	42.3	31.2
160	36.8	35.9
170	31.3	40.7
180	25.7	45.4
184	23.5	47.3
200	14.7	54.8

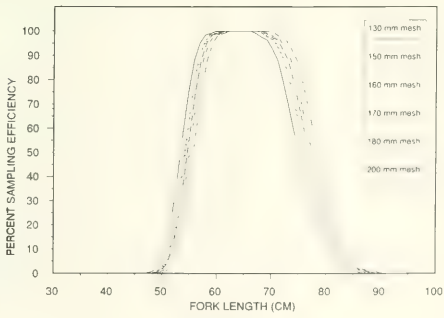

Figure 7

Selectivity curves (%) for albacore *Thunnus alalunga* for 130 mm, 150 mm, 160 mm, 170 mm, 180 mm, and 200 mm stretch-mesh sizes.

percent efficiency of sampling at the 53 cmFL peak was regressed against mesh size for all mesh sizes (Fig. 6). The estimated percent sampling efficiency at 53 cmFL for each mesh size is shown in Table 2. Using the same method, the percent sampling efficiency was estimated for 78 cmFL for each mesh size (Fig. 6, Table 2).

The family of selectivity curves by mesh size is shown in Fig. 7. These were determined by shifting the mean selectivity-curve limbs to the left or right so that sampling efficiencies at 53 and 78 cmFL matched the values in Table 2 for each mesh size. Fork lengths between the two limbs were assumed to be sampled with maximum efficiency, consistent with theory associated with unimodal selectivity curves (Hamley 1975).

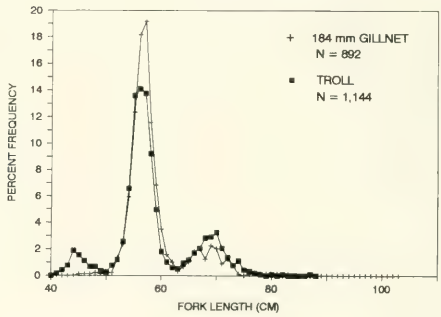

Figure 8

Percent frequency-of-occurrence by fork-length interval for albacore *Thunnus alalunga* sampled in the 1985 NMFS experiment by 184mm stretch mesh and by trolling.

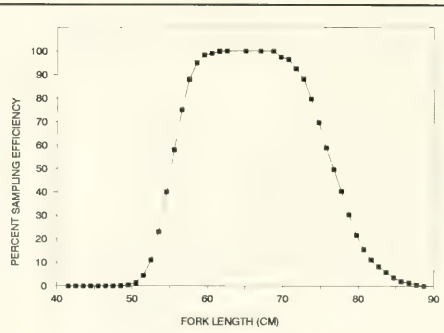

Figure 9

Selectivity curve for albacore *Thunnus alalunga* for 184 mm stretch-mesh size.

NMFS 1985 experiment

Length-frequency data for albacore collected in the 184 mm mesh during the 1985 NMFS experiment are shown in Fig. 8. The estimated selectivity curve is shown in Fig. 9 and, as expected, is almost identical to the 180 mm mesh selectivity curve (Fig. 7). For comparison, length-frequencies from the NMFS experiment taken by both trolling jigs and drift netting in the same area are shown in Fig. 8. As predicted by the selectivity curve (Fig. 9), few fish <50 cm length were sampled by the 184 mm mesh even though the fish were assumed available to the net, as indicated by the size-frequency sampled by the trolling gear fished in the same area and time.

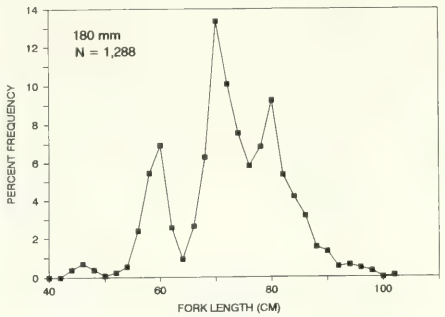

Figure 10
Percent frequency-of-occurrence by fork-length interval for albacore *Thunnus alalunga* for 180mm stretch mesh sampled by the 1982 JAMARC survey (JAMARC 1985).

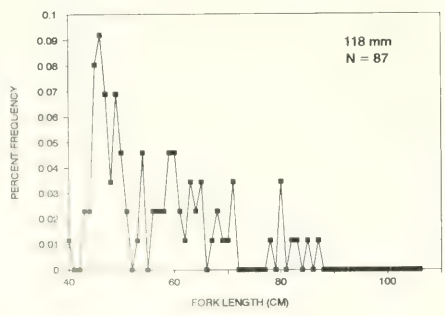

Figure 11
Percent frequency-of-occurrence by fork-length interval for albacore *Thunnus alalunga* for 118mm stretch mesh sampled by the 1983 JAMARC survey (JAMARC 1986).

JAMARC 1982 experiment

The 1982 JAMARC South Pacific experiment collected data for a 180 mm mesh size. Length-frequency data obtained are shown in Fig. 10. The estimated selectivity curve for this mesh is the same as shown for the 180 mm mesh in Fig. 7. From inspection of the length-frequencies for 180 mm and 184 mm mesh sizes from the North Pacific, it was apparent that the South Pacific experiment sampled an albacore population with a different size structure. The results show a much greater proportion of fish in the 70–80 cmFL range than in the North Pacific sampling. This is also seen in samples taken from the U.S. troll fishery that operated in the South Pacific (Rensink 1991)

JAMARC 1983 experiment

Length-frequency data obtained from the 1983 JAMARC South Pacific experiment using 118 mm mesh are shown in Fig. 11. The selectivity relationships developed from the North Pacific data do not accurately predict the expected selectivity curve for the 118 mm mesh. This is a result of small sample sizes and an observed peak size mode well below the sizes of albacore captured in the mesh sizes used to derive the selectivity curves.

Discussion

Selectivity curves derived from the JAMARC 1980 experimental data appear similar in shape to selectivity curves presented for salmon *Onchorynchus nerka* and *O. keta*, slender tuna *Allothunnus fallai*, and mackerel *Scomberomorus niphonius*, and other fusiform fishes (Taguchi 1961, Ishida 1964, Shimazaki et al. 1984). The asymmetry of each selectivity curve (i.e., steeper on the left limb and flatter on the right limb) is similar to that observed for selectivity curves of other fusiform fishes (Hamley 1975) and is explained by the mechanics of capture. The smallest fish, retained by the net at some particular girth/mesh-perimeter ratio, tend to be caught near maximum girth. Also, the range of sizes providing the ratio is relatively narrow. For larger fish, the same ratio can be found over a larger range of fish sizes because the point of capture may be anywhere from the maximum girth forward to the snout tip. For example, maximum girth of albacore increases more rapidly than opercular girth as a function of length (Fig. 12) which extends or skews the

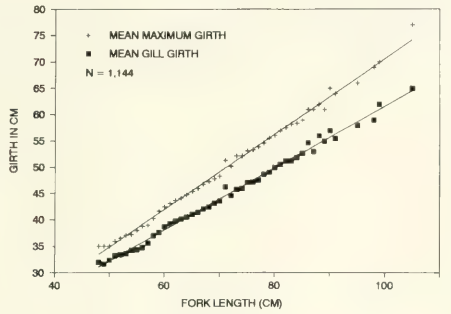

Figure 12
Relationship of albacore *Thunnus alalunga* maximum and opercular girths to fork length for 1144 fish sampled by the 1985 NMFS experiment.

right limb of the selectivity curve. This skewing can be troublesome when symmetrical or pre-determined selectivity curves are fit to data. The method used in this study minimizes this problem.

Assumptions that selectivity curves estimated from the 1980 JAMARC experiment applied to similar nets, such as the NMFS 184 mm mesh and the JAMARC-1982 180 mm mesh, appear acceptable from the data available. The principal factor limiting the application of these selectivity curves to other albacore populations is the girth/length relationships discussed above (Fig. 12). Significant changes in this relationship will change the steepness of the selectivity-curve limbs and the skewness.

Extrapolation of the mean selectivity curve to smaller mesh sizes than those providing the initial data may be improper based on the data observed for the 118 mm mesh. Although the sample size was relatively small, the apparent increase in tangling of larger fish caught in smaller mesh sizes compared with larger mesh sizes suggests that the right portion of selectivity curves for meshes <130 mm are more skewed. Tangled fish did not appear to be a problem in the NMFS or JAMARC 1980 datasets, presumably because all mesh sizes either gilled or wedged fish in the largest mode. Additionally, there may have been fewer larger fish available in the survey areas, as shown by troll-caught samples.

The absence of larger, tangled fish in both net-caught and troll-caught samples could result from reduced availability or vulnerability of larger fish in the areas sampled. Surface fisheries (i.e., drift net, troll, and pole-and-line) for albacore in the North Pacific produce catches with similar length-frequencies in the same areas (Bartoo & Foreman In press). However, albacore taken by subsurface longline gear at the same time and area are generally larger in length than those taken in the surface fisheries. This indicates albacore show differential availability or vulnerability between surface and subsurface gears. This could be due to spatial separation or behavior which may change with fish size. The results presented here assume that vulnerability to DGNs is relatively static over time.

Acknowledgments

We acknowledge contributions to this work by several individuals. Thanks to Tony West and the crew of the F/V Steelfin II for their assistance during the cruises. Thanks to Earl Weber for helping conduct the NMFS drift gillnet experiment, Sonee Sonu for providing Japanese-English translations, and to the many reviewers for constructive comments on the manuscript. Finally, thanks to Karen Handschuh for production of the manuscript.

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Stage-I zoeae of laboratory-hatched *Lopholithodes mandtii* (Decapoda, Anomura, Lithodidae)

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Of the approximately 25 species of Lithodidae of the northern North Pacific Ocean, larvae have been described, at least in part, for 11 species: *Dermaturus mandtii* Brandt, *Cryptolithodes typicus* Brandt, *Hapalogaster grebnitzkii* Schalfeew, *H. mertensii* Brandt, *Lithodes aequispina* Benedict, *Paralithodes brevipes* (Milne Edwards and Lucas), *P. camtschaticus* (Tilesius), *P. platypus* Brandt, *Placetron wosnessenskii* Schalfeew, *Rhinolithodes wosnessenskii* Brandt, and *Hapalogaster dentata* (De Haan). A review of the published descriptions of these larvae, except *H. dentata*, has been given by Haynes (1984). In this paper I describe and illustrate Stage-I zoeae of *Lopholithodes mandtii* Brandt and compare its morphology with the larvae reviewed by Haynes and with the published description of *H. dentata*.

Methods

Zoeae were hatched in the laboratory by an ovigerous female collected 4 April 1989 at Little Port Walter, southern Baranof Island, Alaska. The female was transported to the Auke Bay Laboratory 14 April 1989 and kept in an aquarium with running seawater. The zoeae began hatching about 2 wk later and were active swimmers, congregating near the surface of the aquarium. About 25 of the hatched zoeae were preserved every 2 or 3 d during 2–31 May 1989, until no zoeae remained alive in the aquarium. No attempt was made to rear the zoeae. Water temperatures in the aquarium were 5.6–6.5°C during collection of the larvae. No prezoeae were seen. None of the zoeae collected had molted to Stage II and no morphological differences were noted among the zoeae studied.

Methods of measuring zoeae and their appendages and techniques of illustrations follow Haynes (1984). Processes on the telson are numbered from the outermost to innermost (medial) pair. For clarity in the illustrations, setules on plumose setae and spinules on telsonal spines are omitted, but spinulose setae are shown. At least 5 zoeae were used to verify segmentation and setation; 10 zoeae were used for carapace and total length measurements.

Description of zoeae

Carapace (Fig. 1A,B) Mean carapace length, 1.3 mm (range 1.1–1.5mm); mean total length (excluding telsonal processes), 5.7mm (range 5.1–6.0 mm). Carapace with medially curved, long (>1/4 carapace length) posterolateral spines, and pronounced dorsal ridge. No supraorbital spines. Eyes sessile.

Antennule (Fig. 1C) First antenna (antennule) with unsegmented tubular portion (peduncle) and distal conical projection. Peduncle with ventral plumose seta. Conical projection with 5–6 aesthetascs and a simple seta terminally and two aesthetascs subterminally.

Antenna (Fig. 1D) Antenna with endopod and scale. Endopod slightly shorter than scale, and tipped with two hook-like projections. Antennal scale unsegmented, with fringe of 9 heavily plumose setae along terminal inner margin and prominent spine on distal outer margin. Ventral surface of protopodite with spinulose spine at base of endopod and naked spine at base of antennal scale.

Mandibles (Fig. 1E) Incisor process of right and left mandibles tooth-like with minute serrations. Right mandible: anterior margin with small teeth and denticulated projection; dorsal margin of molar with two denticular ridges; posterior margin with two denticulated projections. Left mandible: anterior margin with premolar denticles. Mandibles without subterminal processes, movable premolar denticle, palp, or palp bud.

Maxillule (Fig. 1F) Endopod 3-segmented, with 3 setae terminally, long distal seta on second segment, and short distal seta on 1st segment; coxal endite unsegmented with 4 plumodenticulate setae and 3 setae subterminally that sometimes have either a few minute spinules or setules; basal endite with 2 elongate, spinelike teeth armed with small denticles and 2 naked setae subterminally; no fine hairs on maxillule.

Maxilla (Fig. 1G) Endopod bilobed, setation formula 3,1,3; basal and coxal endites bilobed; coxal endite with 7 (sometimes 6) terminal and 1 subterminal setae on proximal lobe, 3 terminal and 1 subterminal setae on distal lobe, basal endite with 4 terminal and 1 subterminal setae on proximal lobe and 3 terminal and 1 subterminal setae on distal lobe; scaphognathite with 4 long, marginal plumose setae; fine

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hairs on outer margin of endopod and proximal lobe of coxal endite.

Maxilliped 1 (Fig. 1H) No coxal setae, setation formula of basipod 2,2,3,3; endopod 5-segmented, setation formula 3,2,1,2,4+I (Roman numeral denoting subterminal seta); exopod partially segmented with 4 plumose natatory setae; endopod barely longer than exopod.

Maxilliped 2 (Fig. 1I) No coxal setae; basipod with 1 distal thin spine, armed with marginal spinules plus 1 naked seta and a naked seta in proximal half; endopod 4-segmented, first 3 segments each with distal thin spine armed with marginal spinules plus 1 plumose seta, fourth with 4+I plumose setae; exopod incompletely 2-segmented, 4 plumose natatory setae.

Maxilliped 3 (Fig. 1J) Exopod and endopod undeveloped; exopod partially segmented, with 3 undeveloped setae terminally; endopod with undeveloped seta terminally.

Pereopods (Fig. 1K) Poorly developed, without exopods; 1st pereopod bilobed; 5th pereopod arises medially between 1st and 2nd pereopods.

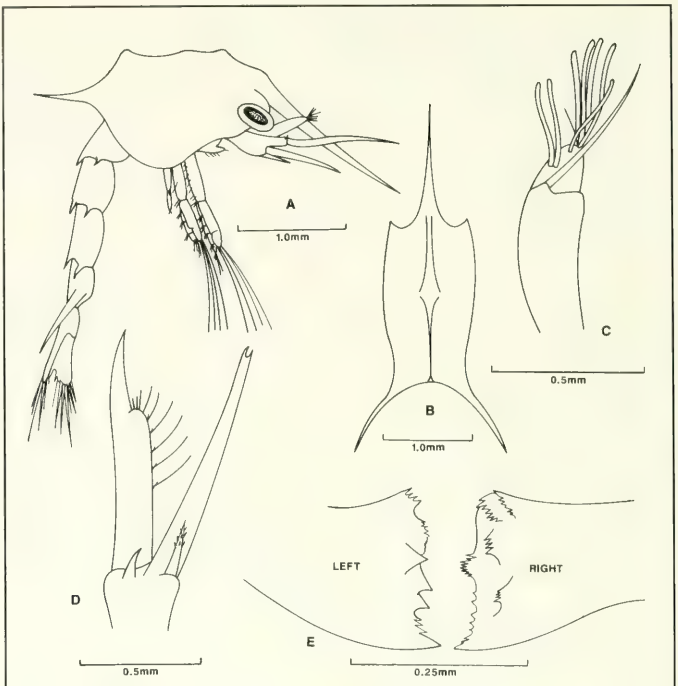

Figure 1
Stage-I zoea of *Lopholithodes mandtii*: **(A)** whole animal, right side; **(B)** carapace, dorsal; **(C)** antennule, ventral; **(D)** antenna, ventral; **(E)** mandibles (left and right), posterior;

Abdomen and telson (Fig. 1L) Abdomen with 5 somites and telson (somite 6 fused with telson); somites 2–4 each with 3 pairs of spines, 2 pairs posterodorsal, 1 pair lateral, lateral pair longest; posterodorsal spines of somite 2 generally equal-sized; median pair of somites 2–4 strongest; lateral pair on somite 5 long (~1.4 times somite width), pointed, somewhat sinuate; telson margin convex with median cleft and 8+8 processes (1,i,3–8), 1st an articulated simple spine, 2nd an anomuran hair (i), 3rd–8th denticulate spines, 4th pair longest, about equal to maximum telson width; all articulated with telson; no uropods or anal spine.

Distinction between *L. mandtii* and other lithodid zoeae

Stage-I zoeae of *L. mandtii* are typical of Stage-I lithodid larvae of the northern North Pacific Ocean as characterized by Haynes (1984). The morphological characteristics of Stage-I lithodid larvae are: sessile eyes and 4 natatory setae each on maxillipeds 1 and 2, maxilliped 3 undeveloped and without natatory setae, pleopods and uropods absent, telson and 6th abdominal somite fused. Lithodid species with typical Stage-I zoeae have 4 zoeal stages. Thus, *L. mandtii* probably has 4 zoeal stages also.

Since the review of lithodid larvae of the northern North Pacific Ocean by Haynes (1984), larvae of *Hapalogaster dentata* have been described by Konishi (1986) who noted that zoeae of *H. dentata* are most similar to those of *Dermaturus mandtii* and can be distinguished from the latter by setation of the antennal scale (7 vs. 10 setae) and the absence of a minute subterminal spine on the antennal endopod in *D. mandtii*. Stage-I zoeae of *H. dentata* are readily distinguished from Stage-I *L. mandtii* by the short (≤1/4 carapace length) posterolateral spines on the carapace and 7+7 telsonal processes.

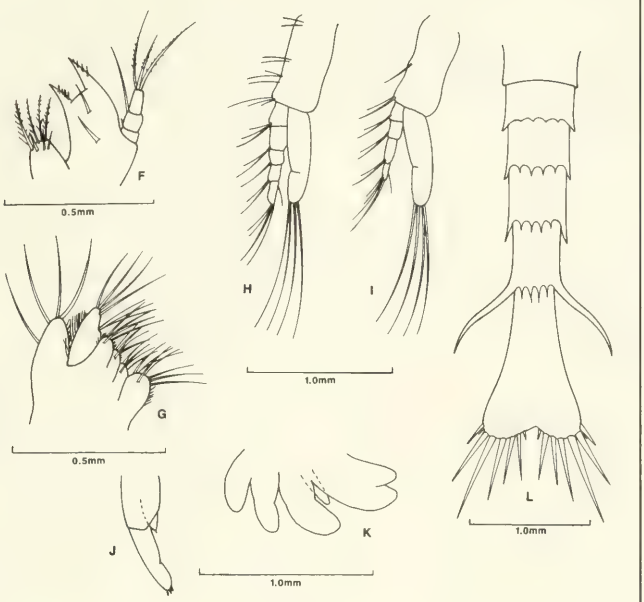

Figure 1

(F) maxillule, ventral; **(G)** maxilla, dorsal; **(H)** maxilliped 1, lateral; **(I)** maxilliped 2, lateral; **(J)** maxilliped 3, lateral; **(K)** pereopods 1–5, lateral; **(L)** abdomen and telson, dorsal.

Comparing Stage-I *L. mandtii* with published descriptions of Stage-I lithodid larvae of the northern North Pacific, they are most similar to Stage-I *Paralithodes camtschaticus*, *P. platypus*, and *Placetron wosnessenskii*. These four species are characterized by a relatively long, pointed rostrum and by relatively long posterolateral spines on the carapace (Sato 1958, Kurata 1964, Makarov 1967, Haynes 1984).

Stage I of *L. mandtii* can be distinguished from *Paralithodes camtschaticus* and *P. platypus* by the shape of the posterolateral spines on the carapace and on somite 5 of the abdomen. In *L. mandtii*, the posterolateral spines on the carapace are slightly longer and have more outward curvature, and the posterolateral spines on somite 5 are longer and more sinuous than in *P. camtschaticus* or *P. platypus*. Also, Stage-I *P. camtschaticus* has fewer plumose setae on the antennal scale than Stage-I *L. mandtii* (5 vs. 9), and Stage-I *P. platypus* has 9+9 telsonal processes rather than 8+8.

Stage-I *L. mandtii* can be distinguished from Stage-I *Placetron wosnessenskii* by general appearance and spination of the abdomen and telson. Individuals of the latter species are noticeably more rugose; the carapace is more heavily ridged and the rostrum is deeper than in Stage-I *L. mandtii*. In Stage-I *P. wosnessenskii* the abdominal spines are relatively long (those of abdominal somite 2 are one-half the length of abdominal somite 3), wide, and blunt, whereas in Stage-I *L. mandtii* the abdominal spines are short (those of somite 2 about one-third the length of somite 3), narrow, and pointed. Also, the telson of *P. wosnessenskii* has 7+7 terminal processes whereas the telson of *L. mandtii* has 8+8 terminal processes.

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Optimal sampling design for using the age-length key to estimate age composition of a fish population

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An age-length key (ALK) is the traditional method for estimating age composition of an application of fish population. Tanaka (1953) showed that the ALK method is a double-sampling technique (Cochran 1977). The first stage uses simple random sampling to collect a very large, but relatively inexpensive, length sample. The second stage subsamples a small number of fish from the first-stage length samples for relatively costly age determination (age subsample). Age subsampling in the second stage can be taken in two fundamental ways, one in which age subsamples are randomly taken from the entire first-stage length samples (random-age subsampling; Kimura 1977) and another in which age subsamples are taken from each stratified length-stratum (stratified-age subsampling; Tanaka 1953). In stratified-age subsampling, fixed-age subsampling (a constant number of age specimens is taken at each length-stratum) and proportional age subsampling (age specimens is proportional to the random length-frequency) are the most popular (Ketchen 1949). However, a general stratified-age subsampling (number of age specimens varied at each length-stratum) can also be used. Stratified-age subsampling is the major focus of this paper. The similarities in results obtained from proportional and random-age subsamplings are given in the Discussion.

This paper was motivated by two articles, Lai (1987) and Jinn et al. (1987), using optimal sampling designs to estimate age composition of a fish population using ALK. The two articles differ significantly. Lai (1987) was based on the classic double-sampling technique and derived the optimal allocation of length samples and age subsamples using Kimura's Vartot (Kimura 1977) and the Cauchy-Schwartz inequality (Kendall & Stuart 1977) for fixed-age subsampling and proportional-age subsampling. Lai (1987) incorrectly used random-age subsampling for proportional-age subsampling. In contrast, Jinn et al. (1987) used a Bayesian approach to estimate age composition, variance, and covariance for a general stratified-age subsampling. They used the iterative method of Roa & Ghangurde (1972) to obtain the optimal allocation of length samples and age subsamples for each length-stratum, with a set of known per-unit costs for ageing a fish in each stratum.

The length-based optimal sampling design of Jinn et al. (1987) has advantages. Because the age of a fish can be expressed as a function of its length (e.g., a von Bertalanffy growth relationship) and because older fish are more difficult to age, the per-unit cost of ageing a fish can be used to estimate the difficulty of ageing older (larger) fish. In addition, the covariance components are important statistics because the sum of all age proportions equals 1, indicating that the estimates of age composition are not mutually independent. The disadvantage of the Bayesian approach of Jinn et al. (1987) is that their method is mathematically complicated and does not provide explicit expressions for the optimal allocations of length and age samples for an ALK, and thus requires substantial computing effort.

The purpose of this paper is to derive a length-based optimal sampling design for an ALK using a classic double-sampling technique. The covariance of age composition also is derived using the method of Kimura (1977). This paper also provides answers to the question many fishery scientists have asked me: What is the explicit solution to a length-based optimal sampling design for an ALK? A discussion on the general applicability of ALK in the sampling program with complexity of fishery-time-areal stratification and tows/trips clusterization is also provided.

Methods

I use the following notation for an ALK with a general stratified-age subsampling:

- N = total number of length samples;
- N_i = number of fish in the ith length-stratum, i=1,...,L;
- l_i = proportion of fish in the ith length-stratum, ($\hat{l}_i = N_i/N$);
- n_i = number of age sub-samples randomly taken from the ith length-stratum;
- n_{ij} = number of fish from n_i assigned to the jth age-class;
- q_{ij} = proportion of fish in the ith length-stratum that fall into the jth age-class ($\hat{q}_{ij} = n_{ij}/n_i$);
- A = number of age-classes;
- L = number of length-strata;
- p_j = proportion of population in the jth age-class;

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Fishery Bulletin, U.S. 92:382-388 (1993).

$\mathrm{Var}(p_j)$ = variance of p_j ;
$\mathrm{Cov}(p_j,p_k)$ = covariance between p_j and p_k.
A caret denotes the estimate of each variable.

The unbiased estimate of p_j (Tanaka 1953) from an ALK is

$$\hat{p}_j = \sum_{i=1}^{L} \hat{l}_i \hat{q}_{ij} . \qquad (1)$$

The variance of $\hat{p}_j$ has been derived by Tanaka (1953) and Kimura (1977); however, the approximate form of variance is more frequently used (Kutkuhn 1963, Southward 1963, Doubleday & Rivard 1983, Lai 1987):

$$Var(\hat{p}_j) \approx \sum_{i=1}^{L} \left[\frac{\hat{l}_i^2 \hat{q}_{ij}(1-\hat{q}_{ij})}{n_i} + \frac{\hat{l}_i (\hat{q}_{ij}-\hat{p}_j)^2}{N} \right]. \qquad (2)$$

The terms in the right-hand side of Eq. 2 represent the portion of the total variance due to variation within length-strata and that due to variation between strata, respectively.

The covariance of $\hat{p}_j$ and $\hat{p}_k$ is derived using the method of Kimura (1977):

$$Cov(\hat{p}_j,\hat{p}_k) = \sum_{i=1}^{L} \frac{-\hat{l}_i(1-\hat{l}_i)\hat{q}_{ij}\hat{q}_{ik}}{Nn_i} + \sum_{i=1}^{L} \frac{-\hat{l}_i^2 \hat{q}_{ij}\hat{q}_{ik}}{n_i} + \sum_{i=1}^{L} \frac{\hat{l}_i \hat{q}_{ij}\hat{q}_{ik}}{N} - \frac{\hat{p}_j\hat{p}_k}{N}$$

$$\approx \sum_{i=1}^{L} \frac{-\hat{l}_i^2 \hat{q}_{ij}\hat{q}_{ik}}{n_i} + \sum_{i=1}^{L} \frac{\hat{l}_i \hat{q}_{ij}\hat{q}_{ik}}{N} - \frac{\hat{p}_j\hat{p}_k}{N} . \qquad (3)$$

The approximate form of covariance omits the first term because this term is small compared with the sum of the other two terms. A quadratic loss function (Jinn et al. 1987) is used to infer the precision of the estimated age composition $\hat{\mathbf{p}}'=(\hat{p}_1,\hat{p}_2,\ldots,\hat{p}_A)$:

$$\mathcal{L}(\hat{\mathbf{p}},\mathbf{p}) = (\hat{\mathbf{p}}-\mathbf{p})'\mathbf{W}(\hat{\mathbf{p}}-\mathbf{p})$$
$$= \sum_{j=1}^{A} w_{jj} Var(\hat{p}_j) + \sum_{j\neq k}^{A} w_{jk} Cov(\hat{p}_j,\hat{p}_k)$$
$$= E\left[\sum_{j=1}^{A} w_{jj}(\hat{p}_j-p_j)^2\right] + E\left[\sum_{j\neq k}^{A} w_{jk}(\hat{p}_j-p_j)(\hat{p}_k-p_k)\right]. \qquad (4)$$

The loss function presented in Eq. 4 is identical to Kimura's Vartot provided that $\mathbf{W}$ is an identity matrix, i.e., $w_{jj}=1$ and $w_{jk}=0$ for $j\neq k$.

Substituting Eq. 2 and the approximate form of Eq. 3 into Eq. 4 and collecting terms, we obtain:

$$\mathcal{L} = \sum_{i=1}^{L} \left(\frac{a_i-u_i}{n_i} \right) + \frac{b+v-m}{N} , \qquad (5)$$

where $a_i = \sum_{j=1}^{A} w_{jj} \hat{l}_i^2 \hat{q}_{ij}(1-\hat{q}_{ij})$,

$u_i = \sum_{j\neq 1}^{A} w_{jk} \hat{l}_i^2 \hat{q}_{ij}\hat{q}_{ik}$,

$b = \sum_{i=1}^{L} \sum_{j=1}^{A} w_{jj} \hat{l}_i (\hat{q}_{ij}-\hat{p}_j)^2$,

$v = \sum_{i=1}^{L} \sum_{j\neq k}^{A} w_{jk} \hat{l}_i \hat{q}_{ij} \hat{q}_{ik}$.

$m = \sum_{j\neq k}^{A} w_{jk} \hat{p}_j \hat{p}_k$,

and where a_i, u_i, b, m, and v are all positive.

A linear cost function is used for the optimal sampling design:

$$C = c_1 N + \sum_{i=1}^{L} c_{2i} n_i , \qquad (6)$$

where C is total cost, c_1 is per-unit cost of collecting a random length sample, and c_{2i} is per-unit cost for ageing a fish in the ith length-stratum.

Survey designs generally are based on two constraints: (i) a fixed total cost, i.e., minimize the loss function in Eq. 4 at a fixed cost; or (ii) a desired precision of the estimators, i.e., minimize the total cost at a given level of the loss function. Therefore, the problem for optimal allocation becomes one of determining the optimal set of N^* and n_i^*'s which minimizes L at a given total cost or which minimizes total cost at a desired precision level of L (N^* and n_i^* are the optimal sample sizes of length and age samples, respectively). Kendall & Stuart (1977, Sect. 39.20) and Cochran (1977, Sect. 5.5) show that choosing the optimal set of N^* and n_i^*'s to minimize L for a fixed C or to minimize C for a fixed L are both equivalent to minimizing the product of L and C:

$$\mathcal{L}C = \left[\sum_{i=1}^{L} \frac{a_i-u_i}{n_i} + \frac{b+v-m}{N} \right] \left[c_1 N + \sum_{i=1}^{L} c_{2i} n_i \right]. \qquad (7)$$

Applying the Cauchy-Schwarz inequality to Eq. 7, the product LC is

$$\mathcal{L}C = \left[\sum_{i=1}^{L} \left(\sqrt{\frac{a_i-u_i}{n_i}} \right)^2 + \left(\sqrt{\frac{b+v-m}{N}} \right)^2 \right] \left[(\sqrt{c_1 N})^2 + \sum_{i=1}^{L} (\sqrt{c_{2i} n_i})^2 \right]$$
$$\geq \left[\sum_{i=1}^{L} \sqrt{c_{2i}(a_i-u_i)} + \sqrt{b+v-m} \right]^2 .$$

Kendall & Stuart (1977) showed that the minimum value of the product LC occurs when

$$\frac{\sqrt{c_{21} n_1}}{\sqrt{\frac{a_1-u_1}{n_1}}} = \ldots = \frac{\sqrt{c_{2i} n_i}}{\sqrt{\frac{a_i-u_i}{n_i}}} = \ldots = \frac{\sqrt{c_{2L} n_L}}{\sqrt{\frac{a_L-u_L}{n_L}}} = \frac{\sqrt{c_1 N}}{\sqrt{\frac{b+v-m}{N}}} = \text{constant} > 0 \qquad (8)$$

Use the terms of the equality between the ith and the (L+1)th terms and rearrange the variables to obtain $r_i^* = n_i^*/N^*$, the optimal subsampling ratio between age subsamples and length samples in the ith length stratum. The solution of r_i^* is:

$$r_i^* = \sqrt{\frac{c_1(a_i-u_i)}{c_{2i}(b+v-m)}}. \quad (9)$$

For a survey design subject to a given total cost C, r_i^* is the optimal subsampling ratio required to reach the minimum loss function value (min. $\mathcal{L}$). Thus, substitute Eq. 9 into Eq. 6 and solve for the optimal set of N^* and n_i^*:

$$N^* = \frac{C}{c_1 + \sum_{i=1}^{L} c_{2i} r_i^*},$$

$$n_i^* = r_i^* N^*,$$

$$\text{min. } \mathcal{L} = \sum_{i=1}^{L}\left(\frac{a_i-u_i}{n_i^*}\right) + \frac{b+v-m}{N^*}. \quad (10)$$

For a survey design subject to a desired precision level of $\mathcal{L}$, r_i^* is the optimal subsampling ratio to reach the minimum total cost (min. C). The optimal set of N^* and n_i^* can be obtained by substituting Eq. 9 into Eq. 5:

$$N^* = \frac{1}{\mathcal{L}'}\left[\sum_{i=1}^{L}\left(\frac{a_i-u_i}{r_i^*}\right) + b+v-m\right],$$

$$n_i^* = r_i^* N^*, \quad (11)$$

$$\text{min. } C = c_1 N^* + \sum_{i=1}^{L} c_{2i} n_i^*.$$

Similarly, the above derivation can be extended to the traditional fixed- and proportional-age subsampling schemes. For these age subsampling schemes, the per-unit cost for ageing a fish is not length-specified (i.e., $c_{2i}=c_2$ for all i's). The loss and cost functions in Eq. 5 and 6 are modified according to the definition of the two age subsampling schemes: (1) $n_i=n/L$ for fixed-age subsampling, and (2) $n_i = n\,l_i$ for proportional-age subsampling, where $n = \Sigma n_i$. The loss function for fixed-age subsampling is

$$\mathcal{L}' = \frac{\sum_{i=1}^{L} L(a_i-u_i)}{n} + \frac{b+v-m}{N} \quad (12)$$

and that for a proportional-age subsampling is

$$\mathcal{L}' = \frac{\sum_{i=1}^{L} L(a_i-u_i)/\hat{l}_i}{n} + \frac{b+v-m}{N}. \quad (13)$$

The cost function for both age subsampling schemes is:

$$C = c_1 N^* + c_2 n \quad (14)$$

Using the Cauchy-Schwarz inequality, the optimal subsampling ratio (r*) for either minimizing $\mathcal{L}$ at a fixed total cost C or minimizing total cost C at a desired precision level of $\mathcal{L}$ for a fixed-age subsampling is:

$$r^* = \frac{n^*}{N^*} = \sqrt{\frac{c_1\sum_{i=1}^{L} L(a_i-u_i)}{c_2(b+v-m)}} \quad (15)$$

The optimal set of N^* and n^* and min. $\mathcal{L}$ subject to fixed cost is:

$$N^* = c_1 + c_2 r^*,$$

$$n^* = r^* N^*, \quad (16)$$

$$\text{min. } \mathcal{L}' = \frac{\sum_{i=1}^{L} L(a_i-u_i)}{n} + \frac{b+v-m}{N}.$$

and the optimal set of N^* and n^* and min. C subject to a desired precision level of $\mathcal{L}$ is

$$N^* = \frac{1}{\mathcal{L}'}\left[\frac{\sum_{i=1}^{L}(a_i-u_i)}{r^*} + b+v-m\right],$$

$$n^* = r^* N^*, \quad (17)$$

$$\text{min. } C = c_1 N^* + c_2 n^*.$$

For proportional-age subsampling, the optimal subsampling ratio (r^*) for either minimizing $\mathcal{L}$ at a given total cost C, or minimizing total cost C at a desired precision level of $\mathcal{L}$, is:

$$r^* = \sqrt{\frac{c_1\sum_{i=1}^{L}(a_i-u_i)/\hat{l}_i}{c_2(b+v-m)}} \quad (18)$$

The optimal set of N^* and n^* and min. $\mathcal{L}$ subject to a given total cost C is

$$N^* = c_1 + c_2 r^*,$$

$$n^* = r^* N^*, \quad (19)$$

$$\text{min. } \mathcal{L}' = \frac{\sum_{i=1}^{L}(a_i-u_i)/\hat{l}_i}{n^*} + \frac{b+v-m}{N^*}.$$

and the optimal set of N^* and n^* and min. C subject to a desired precision level of $\mathcal{L}$ is:

$$n^* = \frac{1}{\mathcal{L}^*}\left[\frac{\sum_{i=1}^{k}(a_i - u_i)/\hat{l}_i}{r^*} + (b+v-m)\right],$$

$$n^* = r^* N^*, \qquad (20)$$

$$\text{min. } C = c_1 N^* + c_2 n^* .$$

The solutions given in Eq. 16–20 are similar to that of Lai (1987), provided that the matrix **W** is an identity matrix.

Example

The lemon sole (= English sole *Pleuronectes vetulus*) example of Jinn et al. (1987) is used to illustrate the length-based optimal sampling design. The ALK and per-unit costs are summarized in Table 1. The total cost is C=\$229.15, and the per-unit cost for collecting a length of fish is c_1=\$0.15. For simplicity without loss of generality, consider the special case: w_{jk}=0 for j≠k. Three different sets of w_{jj} are used to reflect different aspects of interest:

Table 1

Age-length key and length-frequency distribution of male lemon sole (= English sole, *Pleuronectes vetulus*) collected from Strait of Georgia, British Columbia. Original dataset is from Ricker (1975:68), and per-unit cost for ageing is from Jinn et al. (1987).

Length stratum (cm)	Number of age sub-samples	Age 4	5	6	7	8	9	Number of length samples	Per-unit cost of ageing
27	6	5	1					6	1.0
28	9	3	4	2				9	1.2
29	10	4	4	1	1			30	1.4
30	10	1	5	4				51	1.6
31	10		8	2				54	1.8
32	10	1	7	1	1			48	2.0
33	10	1	3	3	2	1		41	2.2
34	10		2	6	1	1		27	2.4
35	10		1	4	3		2	13	2.6
36	6			1	3	2		6	2.8
37	3			1	1	1		3	3.0
38	1					1		1	3.2
Age proportion		0.12	0.48	0.26	0.09	0.04	0.01		
Variance ($\times 10^{-3}$)		1.09	2.98	2.46	0.88	0.33	0.04		

Case 1 {1,1,1,1,1,1}: equal interest in estimating all $\hat{p}_i$'s;

Case 2 {10,30,30,10,1,1}: increase precision of four major age-classes with larger Var($\hat{p}_i$);

Case 3 {1,1,1,1,10,60}: interest in older but rare age-classes.

The results obtained from length-based design are compared with those from fixed- and proportional-age subsampling schemes. The average per-unit cost for ageing a fish (c_2) is calculated as the weighted mean of c_{2i}, which is c_2=\$1.96. The optimal set of {N^*, n_i^*} and min. $\mathcal{L}$ subject to the given total cost of \$229.15 are computed using Eq. 9 and 10 for length-based age subsampling, Eq. 15 and 16 for fixed-age subsampling, and Eq. 18 and 19 for proportional-age subsampling.

Precision improves substantially when length-based age subsampling rather than fixed-age subsampling is used in all three cases (Table 2). In the first two cases, however, precision improves marginally by using length-based age rather than proportional-age subsamplings. When rare and older fish (ages 8 and 9, Case 3) are of interest, precision is substantially improved by using length-based age instead of proportional-age subsampling. This is due to the fact that proportional-age subsampling is not designed to increase age subsamples from length-strata consisting of older age-classes.

The optimal set of {N^*, n_i^*} and min. C subject to a desired precision level of $\mathcal{L}^*$=0.01 are computed from Eq. 9 and 11 for length-based age subsampling, Eq. 15 and 17 for fixed-age subsampling, and Eq. 18 and 20 for proportional-age subsampling. Tables 2 and 3 show similar trends. The cost efficiency of length-based age subsampling is superior to fixed-age subsampling in all cases. However, cost efficiency is only marginally

Table 2

Optimal sample sizes of length and age samples and min. $\mathcal{L}$ ($\mathcal{L}$: loss function) subject to fixed total cost, C=$229.15, for three different age subsampling schemes. Age-length key dataset is listed in Table 1. Per-unit cost of observing a length sample, c_l=$0.15. Case 1 $\{w_i\}$=$\{1,1,1,1,1,1\}$; Case 2 $\{w_i\}$=$\{10,30,30,10,1,1\}$; and Case 3 $\{w_i\}$=$\{1,1,1,1,10,60\}$.

Length (cm)		Case 1	Case 2	Case 3
27		2	2	2
28		4	5	3
29		14	13	10
30		21	23	15
31		15	18	11
32		16	16	12
33		17	16	18
34		9	9	11
35		5	4	13
36		2	1	3
37		1	1	1
38		1	1	1
Length-based sampling design	n*	107	109	100
	N*	183	182	204
	min. $\mathcal{L}$	0.0058	0.1312	0.0110
Improvement of precision (%)[1] vs.				
Fixed-age subsampling		36.26	39.15	28.57
Proportional-age subsampling		4.92	4.23	19.12
Fixed-age subsampling	n*	106	106	104
	N*	146	141	172
	min. $\mathcal{L}$	0.0091	0.2156	0.0154
Proportional-age subsampling	n*	103	103	103
	N*	179	177	183
	min. $\mathcal{L}$	0.0061	0.1370	0.0136

[1] % = percent difference of min. $\mathcal{L}$ between length-based sampling design and fixed or proportional-age subsampling.

Table 3

Optimal sample sizes of length and age samples and minimum total cost (min. C) subject to a desired precision level of loss function, $\mathcal{L}$=0.01 for the three different age subsampling schemes. Age-length key dataset is listed in Table 1. Per-unit cost of observing a length sample, c_l=$0.15. $\{w_i\}$ for each case are the same as that in Table 2.

Length (cm)		Case 1	Case 2	Case 3
27		1	3	2
28		3	6	4
29		8	17	11
30		12	30	17
31		9	23	12
32		9	21	13
33		10	21	20
34		5	12	12
35		3	5	14
36		1	2	3
37		1	1	2
38		1	1	1
Length-based sampling design	n*	63	142	111
	N*	106	236	223
	min. C	135.98	300.6	257.25
Cost efficiency (%)[1] vs.				
Fixed-age subsampling		35.14	39.09	27.06
Proportional-age subsampling		1.08	3.68	17.33
Fixed-age subsampling	n*	97	229	160
	N*	133	304	265
	min. C	209.66	493.48	352.68
Proportional-age subsampling	n*	62	141	140
	N*	108	242	249
	min. C	137.46	312.07	311.16

[1] % = percent difference of min. C between length-based sampling design and fixed- or proportional-age subsampling.

different between length-based age and proportional age subsamplings in Cases 1 and 2. In Case 3, the cost efficiency of length-based age subsampling increases subtantially over proportional-age subsampling.

Discussion

To draw a general conclusion, many different sets of w_i's and full matrices of **W** also were investigated. The results from these additional analyses were similar to that of Tables 2 and 3. In general, the length-based age subsampling is superior to either fixed- or proportional-age subsampling. However, precision improvement and cost efficiency depend on the weights placed on particular age-classes. Total cost will change in accord with the different weights and desired precision. A higher total cost should be allowed for cases where sampling is designed to improve the precision of highly variable estimates, usually young and old age-classes.

A larger budget will increase precision of the estimates, especially for highly variable age-classes; however, as Lai (1987) showed, there is a point of diminishing returns as the budget increases (Fig. 1). For the examples used in this paper, precision improvement is marginal when total cost (C) increased beyond $40 for Cases 1 and 3, and beyond $120 for Case 2. Kimura (1989) showed that satisfactory results from cohort analysis can be obtained at low sampling levels (i.e., total cost) provided that the representativeness of the samples can be maintained.

It is difficult to compare the methods of Jinn et al. (1987) with those of this paper because the Bayesian approach and classic sampling techniques are derived from different theoretical backgrounds. Nontheless, the results obtained from this paper are similar to that of

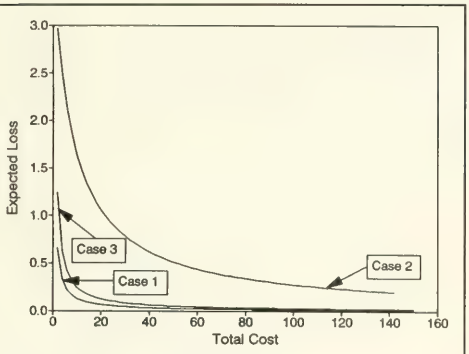

Figure 1

Relationship between minimum loss function value and total cost for the lemon sole (= English sole *Pleuronectes vetulus*) example. The relationship can be obtained from substituting N^* and n_i^* in Eq. 10 into the third equation in Eq. 10.

Jinn et al. (1987) although the values of N^* and n_i^* are different. An advantage of the classic double-sampling technique is the explicit solutions of the optimal set of N^* and n_i^*, which reduces computational effort.

In this paper, the optimal sampling design is for stratified-age subsampling. For random-age subsampling in which the number of age subsamples (n) is randomly taken from the entire length sample of size N, the estimated variance and covariance (Kimura 1977) are

$$Var\,(\hat{p}_j) = \sum_{i=1}^{L_k} \left[\frac{\hat{l}_i \hat{q}_{ij}\,(1-\hat{q}_{ij})}{n} + \frac{\hat{l}_i (\hat{q}_{ij}-\hat{p}_j)^2}{N} \right]$$

and

$$Cov\,(\hat{p}_j, \hat{p}_k) = \sum_{i=1}^{L_k} \frac{-\hat{l}_i \hat{q}_{ij} \hat{q}_{ik}}{n} + \sum_{i=1}^{L_k} \frac{\hat{l}_i \hat{q}_{ij} \hat{q}_{ik}}{N} - \frac{p_j \hat{p}_k}{N} .$$

These two equations are similar to that of proportional-age subsampling in which $n_i = n\hat{l}_i$ is substituted into Eq. 2 and 3. However, the estimated variance and covariance for proportional-age subsampling are approximate, and those for random-age subsampling are not. The similarities of random- and proportional-age subsamplings can be anticipated because N is a random sample from a population so that $E(\hat{l}_i) = E(N_i/N) = l_i$, and n is randomly taken from N so that $E(n_i/n) = N_i/N$. This indicates that the size of each n_i will be approximately proportional to l_i, i.e., $n_i/n \approx N_i/N \approx \hat{l}_i$ and $n_i \approx n \cdot l_i$ (Kutkuhn 1963).

An ALK requires a large random sample of fish from which a length-stratified subsample is collected for ageing. Most fishery data are collected either from surveys in which fish from different tows are sampled or from commercial catches in which fish from different vessel-trips are sampled. Pooling data over such clusters is necessary because of the cost of data gathering. In addition to cluster sampling, fisheries data are frequently stratified into time-area, fisheries (or gears), and sex strata (Kimura 1989). The question is how to make the optimal sampling design of ALK generally applicable. To address this, the following factors must be considered: (1) Need of stratification, (2) ALK sampling within stratum, and (3) combined-strata estimation.

Westrheim & Ricker (1978) showed the need for stratification. An ALK obtained from a population at a time-interval should not be universally applied to length-frequency datasets from other populations or other time-intervals if growth and survival rates are different among the populations and time-intervals. Therefore, the factors that may result in differences in growth and survival rates should be evaluated, and stratification should account for these factors.

Current sampling programs (e.g., Doubleday & Rivard 1983, Quinn et al. 1983, Kimura 1989) adopted the strategy in which length-frequency data collected from clustered sampling units (e.g., tows or vessel-trips) within a stratum are pooled, from which a length-stratified subsample is collected for ageing. Southward (1963) evaluated an old method (Southward 1963:12) in which a set of length and age data is collected from each landing of a vessel-trip. Because this old method is not developed from a probability sampling design, the within-vessel variability in fish lengths is assumed to be less than between-vessel variability. Southward (1963) showed that this assumption is not valid and the estimated variances of age composition from this old method are so large that little confidence can be placed in it.

The length-frequency data pooled over clusters should be a representative sampling of that stratum. Therefore, the weighting factor of each sample should be included in the pooling. Ignoring the weighting factor will bias the estimated age composition (Kimura 1989). Quinn et al. (1983) described a sampling-rate method in which a fixed proportion of halibut were sampled from landings >1000 lbs for length data, and then age data were subsampled from the pooled length samples from these landings. All length samples are self-weighted and can be pooled directly.

Quinn et al. (1983) evaluated the methods of combined-strata estimation and found that the "project-and-add" method (total catch-at-age is estimated for each stratum and then the estimates are added over

strata; see Quinn et al. 1983) produces unbiased estimators if all strata are sampled. The project-and-add method uses the concept of a stratified, random sampling technique (Cochran 1977). Therefore, Cochran's rules (Cochran 1977:98) of optimal allocation for stratified random sampling can be applied. In a given stratum, take larger length and age samples if (1) the stratum is larger, (2) the stratum is more variable internally, and (3) sampling is cheaper in the stratum. The first two rules are the basis of the Neyman allocation (Cochran 1977:99). The sampling-rate method proposed by Quinn et al. (1983) built upon the first rule and can easily incorporate other rules in the sampling program.

It is clear that the number of strata and variability (vartot or loss function) of each stratum should be evaluated first for designing ALK sampling. Then, the total cost is allocated into various strata according to Cochran's rules. Once the total cost for each stratum is determined, an optimal sampling design for ALK can be applied. The sampling rate method of Quinn et al. (1983) can be used to collect the optimal length sample size from clusters. After pooling the length samples, a length-stratified subsample is collected for ageing.

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Recruitment of bluefish *Pomatomus saltatrix* to estuaries of the U.S. South Atlantic Bight*

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The bluefish *Pomatomus saltatrix* is a pelagic species that is distributed circumtropically (Briggs 1960, Richards 1965, van der Elst 1976, Fable et al. 1981, Pollock 1984, Lenanton & Potter 1987). Ichthyoplankton surveys off the U.S. east coast indicate three separate spawning concentrations of bluefish, namely (1) a spring-spawned cohort produced between March and May in the South Atlantic Bight (SAB), (2) a summer-spawned cohort originating between June and August in the Middle Atlantic Bight (MAB), and (3) a fall-spawned cohort produced in the SAB between September and January (Norcross et al. 1974, Kendall & Walford 1979, Powles 1981, Collins & Stender 1987).

The abundance of bluefish has fluctuated widely along the Atlantic coast during the past century (Baird 1873, Bigelow & Schroeder 1953). Recently, population abundance increased steadily from the early 1960s to the late 1970s (Gilmore 1985) and remained relatively high during the 1980s (NMFS 1987, 1988). Chiarella & Conover (1990) speculated that increased recruitment success of the spring-spawned cohort is largely responsible for this recent increase in overall bluefish abundance. They demonstrated that bluefish off the New York coast during the 1980s were primarily spring-spawned fish, and this contrasts with a more equal proportion of spring-spawned and summer-spawned fish observed by Lassiter (1962) in the late 1950s, when overall bluefish abundance was lower.

Our understanding of how these three intra-annual cohorts contribute to the overall year-class strength of bluefish along the U.S. Atlantic coast, however, is still unclear. For example, Kendall & Walford (1979) hypothesized that spring-spawned bluefish were transported from the SAB northward into the MAB estuaries, but Collins & Stender (1987) postulated that spring-spawned fish were transported directly inshore to estuaries of the SAB. Otolith analyses of young recruits have confirmed the northerly dispersal of spring-spawned fish as proposed by Kendall & Walford (Nyman & Conover 1988, McBride & Conover 1991), but similar studies of recruitment to SAB estuaries are nonexistent. Length-frequency data for bluefish from SAB estuaries is also sparse, thus it has been difficult to evaluate if bluefish use estuaries in the SAB as nursery grounds. Here we present evidence of recruitment by three cohorts of young-of-the-year (YOY) bluefish to estuaries and nearshore habitats of the SAB.

Materials and methods

Field sampling

Bluefish <360mm fork length (FL) were collected from estuarine poundnet (a summer fishery) and oceanic trawl (a winter fishery) samples taken in North Carolina (Table 1). The upper limit of 360mmFL represents the largest size attained by young bluefish in their first year of life (Lassiter 1962). Additional data were also obtained from a variety of fishery-independent sources of sampling from North Carolina to Florida (Table 1).

Otolith aging

To avoid dissolution, sagittal otoliths were extracted directly in the field, or from frozen or preserved (95% ETOH) fish. Nyman & Conover (1988) validated that daily increments are present in otolith microstructure, and we followed their methods of preparation. Sagittae were chosen randomly from YOY specimens of the large fishery collections. Eight of the total 51 sagittae prepared were determined to be yearling fish and were excluded from further analysis. Daily sagittal increments were counted independently three times, and a mean count was considered valid if the range was <10% of the mean count. If the range was greater (11% of the time), then a fourth count was made and the outlier was discarded.

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Table 1

Sources of bluefish *Pomatomus saltatrix* samples examined in this study. Size range is given as mmFL. Larger datasets (n>500) were used to compile length-frequency distributions, and some fish from 1987–88 were used for otolith analyses. Other samples ($n \leq 13$) were obtained specifically for otolith analyses.

Sampling location	*Gear (size & mesh)*	*Sampling period*	*Sample size*	Bluefish *Length range*	*Source**
N.C. estuaries Pamlico and Core Sounds	Otter trawls (3.2 & 6.1m headrope)	March–November 1979–90	547	21–320	NCDMF (Phalen & Stephan 1984)
N.C. estuaries Pamlico Sound Oliver's Reef	Pound-net fishery (Lead 150mm mesh, Tunnel 50mm mesh)	May–November 1982–85	4484	100–360**	NCDMF
N.C. coast Oregon—Beaufort Inlets 4.5–18.5m depths	Trawl fishery (27–33m headrope 400–1400mm wing mesh 50mm cod end mesh)	November–April 1982–85	4466	150–360**	NCDMF
S.C. coast Stono Inlet	Otter trawl (6.1m headrope)	2 November 1988	1	101	NCDMF
S.C. coast Breech Inlet	1×2m neuston net (2 mm mesh)	April–June 1988	9	39–68	SCWMRD
S.C. North Inlet (Town Creek)	Surface trawl	26 July 1988	13	101–123	USC
Nearshore continental shelf Capes Hatteras—Canaveral 4.9–9.1m depths	Falcon trawl (9.1m Mongoose type, 39–45mm stretch mesh)	May–November 1987–88	2276	80–360**	SEAMAP (Wenner 1989)

* Most data and specimens supplied by the N.C. Dep. Mar. Fish. (NCDMF); additional material from S.C. Wildl. Mar. Resour. Dep. (SCWMRD), Univ. South Carolina (USC) Belle Baruch Lab., and the Southeast Area Monitoring and Assessment Program (SEAMAP).

** Data from these sources were truncated at 360mmFL.

Mean ring count (= daily age) was subtracted from date of capture to estimate birthdate, assuming no lag between birthdate and date of first ring deposition. Average growth rate was calculated as ([FL-2mm]/daily age); a 2mm constant represents the size-at-hatching (Deuel et al. 1966). Growth rate was also calculated using least-squares regression of FL on daily age.

Results

Evidence of spring-spawned juveniles Small bluefish (21–60mmFL) entered North Carolina estuaries in March and April (Fig. 1A). These fish were similar in size to spring-spawned bluefish collected by neuston nets on incoming tides at Breech Inlet (South Carolina) as early as 29 April 1988, and as late as 16 June 1988 (Table 2).

This spring-spawned cohort grew rapidly and recruited to the North Carolina pound-net fishery in July (Fig. 1B). These fish became progressively larger until the fishery ended in October. A July recruitment of spring-spawned fish was also evident in SEAMAP trawling (Fig. 1C).

Bluefish <175mmFL in July were YOY that had been spawned primarily in April (Table 2, Fig. 2). For example, a sample from 29 July 1987 had a mean birthdate of 19 April ± 13d (±1SD), and a sample for 26 July 1988 had a mean birthdate of 26 April ± 12d (Table 2). Bluefish observed in July, but >200mmFL, showed evidence of an overwinter growth mark on their otoliths. Very few specimens of 175–200mm were available for otolith analysis, which precluded a more precise separation of age from size modes. Bluefish juveniles were larger and older in August samples (Table 2). Spring-spawned YOY bluefish grew 1.2–1.9mm/d during this time-period (Fig. 3).

Evidence of summer-spawned juveniles Small bluefish (<150–170mmFL) appeared in North Carolina estuaries and in nearshore continental shelf waters of the SAB in October (Fig. 1). Small bluefish (<150mm) collected near Bogue and Stono Inlets in October and November 1988 had a mid-July birthdate (Table 2,

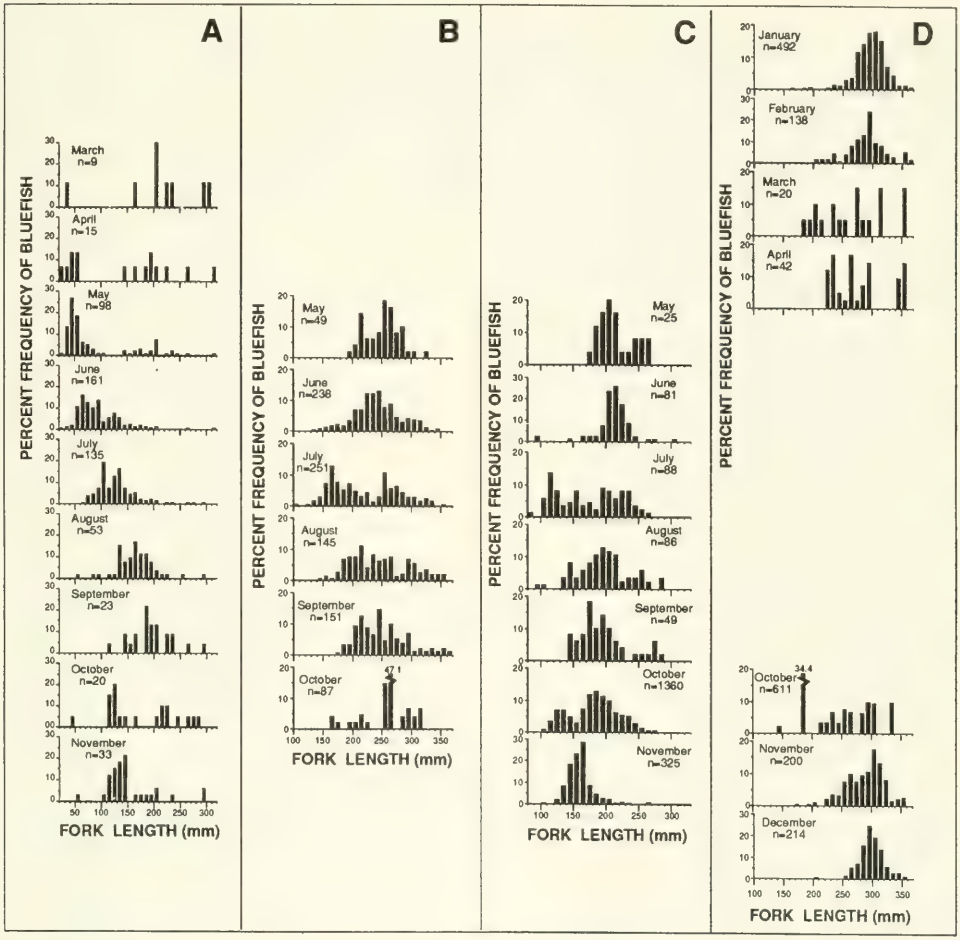

Figure 1

Length-frequency histograms of bluefish *Pomatomus saltatrix* <360mmFL for **(A)** monthly data pooled over the years 1979–90 from a N.C. Dep. Mar. Fish. trawl survey; **(B)** 1984 monthly data from the N.C. summer estuarine pound-net fishery; **(C)** 1988 monthly data from the SEAMAP nearshore trawl survey between N.C. and Florida; and **(D)** 1984–85 monthly data from the N.C. winter oceanic trawl fishery. Years plotted for the last three data sets are representative of data from other years. Ordinates are either 20 or 30%.

Fig. 2). These summer-spawned fish appeared to reach a size similar to that of spring-spawned fish at a common age (Fig. 3), but because they were spawned 2mo later (on average), they were smaller on common sampling dates (Fig. 1A,B,C).

Evidence of fall-spawned juveniles Winter trawl collections did not contain small juveniles between October and January, despite the expectation of an additional length-mode representing fall-spawned fish (Fig. 1D). There was very little evidence of fall-spawned fish in any of the length-frequency data, except possibly two fish (~40–60mmFL) collected in October and November in North Carolina estuaries (Fig. 1A). Based on otolith ageing, a single specimen collected in August was determined to be 206d old (i.e., with a corresponding birthdate of 9 January) which was unique in relation to all other estimated birthdates in this study

Table 2

Descriptive statistics for 43 aged specimens of juvenile bluefish *Pomatomus saltatrix* collected in North and South Carolina (NC and SC). Fork length (mmFL), age (d), and growth rate (GR; mm/d) are given as means. One standard deviation (SD) is provided where more than one specimen was measured.

Collection date	Location	Mean FL	SD	Mean Age	SD	Mean GR	SD	n
			1987					
15 Jun	Pamlico Sound NC	75		74.0		0.986		1
29 Jul	Pamlico River NC	119.6	14.5	101.3	13.1	1.169	0.134	5
13 Aug	Pamlico Sound NC	208		142.0		1.456		1
17 Aug	Pamlico Sound NC	192		125.3		1.516		1
			1988					
29 Apr	Breech Inlet SC	50.7	3.05	62.4	1.21	0.779	1.147	3
17 May	Breech Inlet SC	40		51.3		0.740		1
16 Jun	Breech Inlet SC	57.8	11.9	51.4	7.53	1.079	0.128	5
26 Jul	North Inlet SC	112.7	6.74	91.8	12.0	1.216	0.102	10
2 Aug	Pamlico Sound NC	159.5	37.0	143.6	8.94	1.088	0.206	4
2 Aug	Pamlico Sound NC	220		206		1.058		1
25 Oct	Bogue Inlet NC	118.2	31.3	103.2	12.3	1.128	0.064	10
2 Nov	Stono Inlet SC	101		110.0		0.900		1

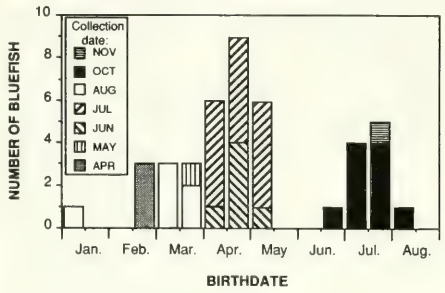

Figure 2

Back-calculated birthdate for 43 YOY bluefish *Pomatomus saltatrix* examined in this study. Date of collection is also shown by month.

(Table 2, Fig. 2) and may have been produced at the tail end of the "fall-spawning" period.

Discussion

Spring-spawned YOY bluefish This cohort recruited to the estuaries of North and South Carolina as early as April and as young as 40d old, and continued to ingress as late as mid-June. Spring-spawned bluefish grew rapidly and appeared in the North Carolina pound-net fishery and in trawls over the nearshore continental shelf in July. Spring-spawned bluefish arrived in SAB estuaries at about the same age (i.e., 40–60d old) but at an earlier first date of estuarine recruitment than in northern estuaries such as New York and New Jersey. Spring-spawned bluefish arrive to the New York Bight no earlier than late May and approximately 60d after hatching (Nyman & Conover 1988, McBride & Conover 1991).

Our findings support Collins & Stender's (1987) hypothesis that at least some spring-spawned YOY bluefish are transported directly inshore and enter estuaries south of Cape Fear. Combined with previous evidence of dispersal north of Cape Hatteras (Nyman & Conover 1988, McBride & Conover 1991), spring-spawned bluefish appear to recruit to estuaries within a broad geographic region encompassing both the SAB and the MAB.

Summer-spawned YOY bluefish This cohort also appeared in estuaries and in nearshore habitats within the SAB. Summer-spawned fish arrived in October at ~100–150mmFL and were generally older than 100d. The presence of these summer-spawned fish in the SAB demonstrates that this cohort migrates from their MAB spawning/nursery grounds into the SAB in the fall. Lund and Maltezos (1970) demonstrated that YOY bluefish tagged in New York migrated to the SAB, but these tagged fish were the larger spring-spawned fish.

Fall-spawned YOY bluefish This cohort was not clearly observed in length-frequency data and, at most,

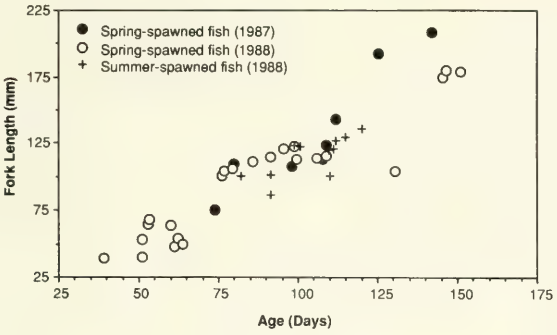

Figure 3

Fork length (FL) as related to daily age of bluefish *Pomatomus saltatrix*, based on samples collected near inlets and within estuaries. Linear regression equations for spring-spawned YOY bluefish were FL= -62.8+1.86(Age) [r^2=0.85] for 1987, and FL= -6.67+1.20(Age) [r^2=0.87] for 1988.

one specimen appeared in our otolith analysis. The winter data used in our study may be inappropriate for sampling fall-spawned bluefish because the trawl fishery uses a large mesh size and fishes in deep water (Table 1). Presumptive fall-spawned YOY fish were uncommon in previous surveys between North Carolina and Florida (Table 3). Wenner & Sedberry (1989) speculated that they had collected fall-spawned fish during January and May trawl collections in nearshore habitat of the SAB, but their interpretation may have been confounded by use of age-length relationships from Wilk (1977). Wilk's growth estimates do not account for intercohort differences in size-at-first-annulus or in growth rates (Lassiter 1962, McBride & Conover 1991). Future analysis of age structure of young bluefish in the SAB should focus on this cohort.

Implications for relative contribution of each cohort We observed polymodal length distributions that represented the size difference between spring- and summer-spawned YOY bluefish cohorts during the fall. Barger (1990) reported that bluefish collected in the SAB had a backcalculated mean FL at Annulus-I of 290mm. This size matches the mean FL at Annulus-I reported for spring-spawned fish from North Carolina in the late 1950s (Lassiter 1962). This observation supports the conclusion that the spring-spawned cohort is of dominant abundance relative to the other cohorts, as interpreted by Chiarella & Conover (1990).

Table 3

Total number of young-of-the-year bluefish *Pomatomus saltatrix* collected in various seining studies from North Carolina to Florida. Number of bluefish is given by month, "Years" refers to the duration of each study, and size range is given in parentheses as mmFL (either as reported or as converted using regressions from McBride 1989). Asterisk indicates that length-frequencies were given as 5mm class-intervals. nd = no data. Sampling frequency ranged from biweekly to bimonthly; seine sizes 12.2–21.3m in length. References: (1) Tagatz & Dudley 1961, (2) Anderson et al. 1977, (3) Cupka 1972, (4) Miller & Jorgenson 1969, (5) Futch & Dwinell 1977.

Location (Ref.)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Years
Beaufort NC (1)	0	0	0	0	1	0	1	0	0	7	12	0	1957–60
Ocean Beach					(46)		(100)			(65–79)	(40–55)		
Beaufort NC (1)	0	0	0	0	0	0	1	0	0	0	0	0	1957–60
Salt Marsh							(136)						
Beaufort NC (1)	0	0	1	0	4	1	1	0	0	0	0	0	1957–60
River			(120)		(66–77)	(86)	(123)						
Folly Beach SC (2)	0	0	0	0	0	1	1	0	0	0	0	0	1969–71
Ocean Beach						(104)	(137)						
Murrells Inlet—	0	0	0	0	0	44	0	0	0	0	0	0	1971
Edisto beaches SC (3)						(69–124)							
St. Simons I. GA	0	3	2	1	7	9	6	3	0	2	0	0	1953–61
Ocean Beach (4)*		(66–85)	(96–125)	(46–50)	(36–90)	(36–95)	(46–70)	(96–125)		(51–60)			
Hutchinson I. FL	2	nd	0	nd	4	nd	3	nd	0	nd	2	nd	1971–73
Ocean Beach (5)	(325–366)				(273–317)		(42–51)				(70–367)		

Fall-spawned fish are the least represented cohort among juveniles and are known mostly from larval surveys (e.g., Kendall & Walford 1979, Collins & Stender 1987). Collins & Stender (1987) reported bluefish larvae <4mm in the SAB to be more abundant in the spring compared with the fall. Other estuarine surveys have collected small bluefish (<100mm) from October–March in the SAB (Table 3) which strongly suggests that at least some fall-spawned fish do recruit to estuaries.

We suggest that the fall-spawned cohort contributes the least, the summer-spawned cohort contributes somewhat more, and the spring-spawned cohort contributes the most to the Atlantic coast bluefish population, at least in recent years. It is not clear why such differences in abundance among cohorts occur nor for how long such differences persist. The spring-spawned cohort may be more abundant because it is spawned at a place and time enabling invasion of estuaries within the SAB, as well as to estuaries as far north as Maine (Targett & McCleave 1974). The fall-spawned cohort may be less abundant, on average, as it is likely to experience colder temperatures and lower food supplies relative to the other cohorts.

Estuaries of the MAB may be more important as nursery grounds for bluefish than are those of the SAB. Summer abundances of spring- and summer-spawned YOY bluefish in New York Bight estuaries are apparently much higher (0.2–6.3 fish/30m seine haul; McBride & Conover 1991) than in the SAB, based on small numbers of bluefish collected during year-long studies in the south (Table 3). Rountree & Able (1992) also found YOY bluefish to be very common (sixth most abundant fish of 63 spp.) in New Jersey marsh creeks, in contrast to much lower relative abundances in similar polyhaline creeks in the SAB (e.g., Cain & Dean 1976). The wide latitudinal distribution and movements of young bluefish, within and between the Middle and South Atlantic Bights, demonstrate the need to monitor and manage bluefish on a large geographic scale (i.e., nearly the entire U.S. Atlantic coast).

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Abstract.—Developmental stages of pygmy poacher, *Odontopyxis trispinosa*, and blacktip poacher, *Xeneretmus latifrons*, are described and illustrated from specimens collected from the northeastern Pacific Ocean. External morphology, pigmentation, and meristic features are described which distinguish larvae of these species from other agonids occurring in these waters.

Postanal pigment patterns, particularly on the caudal finfold, distinguish preflexion larvae. *Odontopyxis trispinosa* larvae possess a semicircular patch of melanophores that covers nearly the entire caudal finfold. The caudal finfold of preflexion *X. latifrons* larvae are void of pigment with the exception of a small patch of melanophores near the ventral margin of the notochord tip. Flexion and postflexion larvae can be distinguished by caudal and anal fin pigmentation, head spination, and adult meristic features.

Development of larval and early juvenile pygmy poacher, *Odontopyxis trispinosa*, and blacktip poacher, *Xeneretmus latifrons* (Scorpaeniformes: Agonidae)

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The family Agonidae is a morphologically diverse group of relatively small, benthic marine fishes. Agonids, commonly called poachers, are characterized by the presence of fused or overlapping bony plates that encase the body. Fifteen genera represented by 25 species occur in the northeastern Pacific (Matarese et al., 1989).

The pygmy poacher *Odontopyxis trispinosa* is a small (to 8.1 cm SL) subtidal agonid distinguished by an elongate body, small vertical spine at the snout tip, and a moderately developed occipital pit divided by a longitudinal ridge. Fin-element counts of *O. trispinosa* are D III-VI, 5-7; A 5-7; P 13-15; V I,2 (Matarese et al., 1989). The blacktip poacher *Xeneretmus latifrons* is a larger (to 19 cm SL) subtidal agonid distinguished by black margins on the dorsal fins and a weakly developed occipital depression (Miller and Lea, 1972; Hart, 1973). Fin-element counts of *X. latifrons* are D VI-VIII, 6-8; A 6-9; P 13-15; V I,2 (Matarese et al., 1989). The presence of spiny scales on the eyeballs distinguishes *X. latifrons* from *X. leiops*. The absence of cheekplates distinguishes *X. latifrons* from *X. triacanthus* (Miller and Lea, 1972; Eschmeyer et al., 1983).

Freeman (1951) hypothesized that these two taxa are closely related phylogenetically and placed them in his subfamily Xeneretminae. The cladistic analysis of Kanayama (1991) demonstrated close relationships between the two taxa which he placed in the subfamily Anoplagoninae.

The geographic range of adult *O. trispinosa* extends from Southeast Alaska to central Baja California. Adult *X. latifrons* occur over a slightly narrower range from Vancouver Island to northern Baja California (Eschmeyer et al., 1983). Both taxa occur at depths of 18–370 m (Miller and Lea, 1972; Hart, 1973). Larval *O. trispinosa* and *X. latifrons* are the most commonly occurring agonids in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collection[1].

[1]Moser, H. G., ed. Guide to the early stages of fishes from the California Current region. Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, CA 92038. In preparation.

Manuscript accepted 26 February 1993.
Fishery Bulletin, 91:397–413 (1993).

Larval development of agonids is poorly known. Washington et al. (1984) and Maeda and Amaoka (1988) reported that formation of most external body parts, including dermal bony plates and spines, begins early in larval development.

Development of the pygmy poacher (*O. trispinosa*) is described for the first time here. Development of *X. latifrons* is clarified based on new material. A partial developmental series (7, 10, 16 mm SL) of *X. latifrons* was previously described by Marliave (1975). Washington et al. (1984) included a single illustration of *X. latifrons* (9.6 mm SL) which differed markedly in appearance from those in Marliave (1975). Matarese et al. (1989) combined the illustrations from both sources to create a complete developmental series. As a result, some confusion exists as to which illustrations in this series are actually those of *X. latifrons* larvae. The following descriptions are the first complete accounts of larval development in the family Agonidae. Characters are presented that permit identification of these larvae from field collections.

Methods

Specimens

Agonid larvae examined in this study were obtained from collections made off the coasts of Baja California, California, Oregon, Washington (including Puget Sound), Southeast Alaska, and the inside passage waters of British Columbia, Canada (Fig. 1). One hundred and thirty-six *O. trispinosa* (4.3–56.0 mm SL) and 77 *X. latifrons* (4.8–79.0 mm SL) were examined. The largest specimens of each taxa were determined to be adults and are not included in the descriptions. Larvae and juveniles of both taxa were collected with dipnets, 60- and 70-cm bongo nets, Isaacs-Kidd midwater trawls,

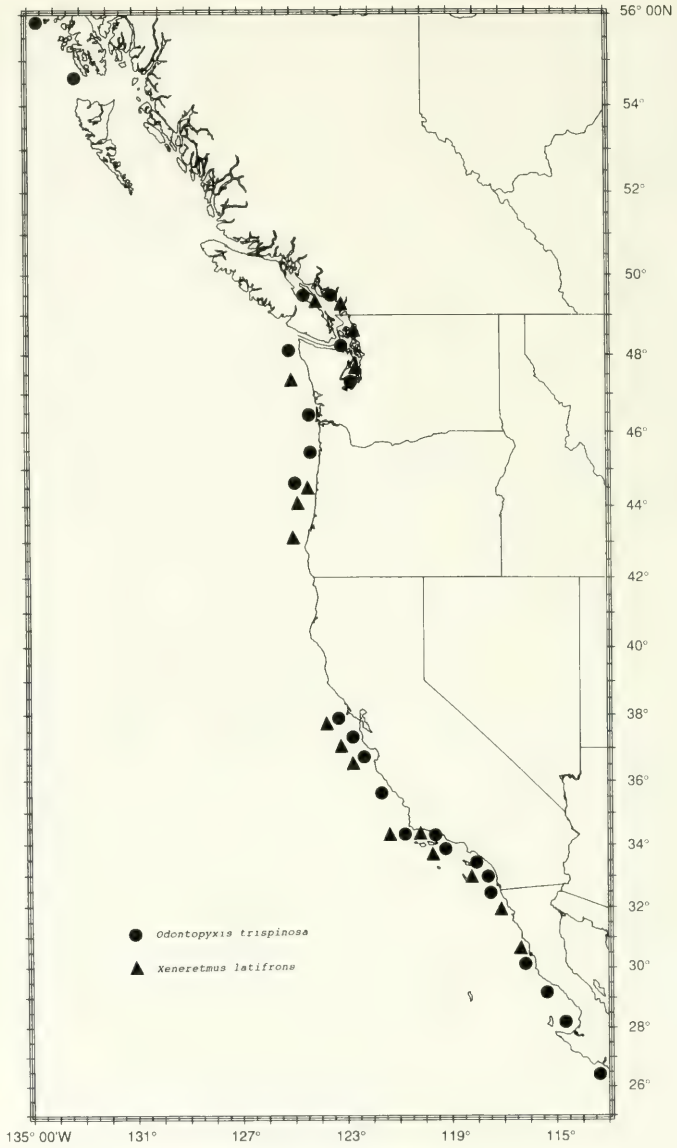

Figure 1

Collection locations of *Odontopyxis trispinosa* and *Xeneretmus latifrons* larvae and early juveniles used in this study.

Tucker trawls, sled trawls, and bottom trawls. Collections were made by the Vancouver Public Aquarium (VPA), Oregon State University (OSU), University of Washington (UW), NOAA's Southwest Fisheries Science Center (SWFSC-CalCOFI program), and the Alaska Fisheries Science Center (AFSC) from the years 1932 to 1991. Specimens are currently housed in the larval fish collections of these institutions. Larvae and juveniles were originally fixed in 3.5 or 5.0% formalin and subsequently transferred and stored in 3.5% buffered formalin or 70% ethanol.

Larvae of *O. trispinosa* and *X. latifrons* were identified using the serial approach. This method uses adult characters to progressively link juveniles to smaller specimens through a continuous sequence of shared similarities. Pigmentation, head spination, body morphology, dermal plates, and meristic features were all used as diagnostic characters. Identification of adult and juvenile specimens was accomplished by using methods of Miller and Lea (1972), Hart (1973), and Kanayama (1991). Nomenclature and taxonomic classification of the family Agonidae follow Kanayama (1991). Developmental series were illustrated by using a camera lucida attached to a dissecting stereomicroscope.

Only melanistic pigmentation is described because formalin fails to preserve color pigments. In the description of pigmentation, the term "band" refers to any aggregation of melanophores that approximates a vertically oriented rectangle. A "bar" also approximates a rectangle but is horizontally oriented. A "patch" is any other distinguishable aggregation of melanophores.

Measurements

The following measurements were made on 45 larvae and early juveniles of *O. trispinosa* and 45 larvae of *X. latifrons* by using an ocular micrometer in a stereomicroscope:

Standard length (SL)—Snout tip to notochord tip prior to development of caudal fin, then to posterior margin of hypural element. (All body lengths in this study are standard lengths.)

Body depth—Vertical distance from dorsal to ventral body margin at pectoral-fin base.

Snout to anus length—Distance along body midline from snout tip to a vertical line through center of anal opening.

Head length (HL)—Snout tip to posterior edge of opercle (to pectoral-fin base in small larvae before opercular margin is visible).

Head width—Distance across head between dorsal margins of orbits.

Snout length—Snout tip to anterior margin of orbit of left eye.

Eye diameter—Greatest diameter of left orbit.

Pectoral fin length—Distance from pectoral-fin base to tip of the longest ray.

Osteology

Selected specimens were cleared and differentially stained to identify cartilage and bone with alcian blue and alizarin red-S (Pothoff, 1984). Skeletal elements and dermal plates were recognized as ossified upon initial uptake of alizarin red-S. Twenty-seven *O. trispinosa* (5.3–41 mm) and 12 *X. latifrons* (7.4–39.2 mm) were cleared and stained for study. Counts of meristic features were made on stained specimens only. Not all stages of development were stained for *X. latifrons* because specimens were limited. Preflexion, flexion, and postflexion stage larvae were stained (Kendall et al., 1984). Nomenclature of skeletal elements follows that used by Leipertz (1985) for *X. triacanthus*. Plate nomenclature follows that of Gruchy (1969) and is described in Figure 2. Terminology of larval head spination follows that proposed for adult

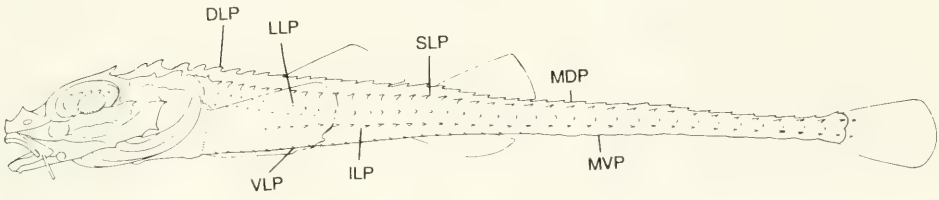

Figure 2
Terminology of bony plates in agonid larvae: DLP=dorsolateral; MDP=mid-dorsal; SLP=supralateral; LLP=lateral line; ILP=infralateral; VLP=ventrolateral; MVP=mid-ventral (after Gruchy, 1969).

agonids by Laroche (1986). For larvae with spines and no named analogous adult spine, terminology follows Moser and Ahlstrom (1978) or Richardson and Laroche (1979) for larvae of rockfish *Sebastes* spp. (another Scorpaeniform) (Table 1, Figs. 3 and 4).

Results

Development of *Odontopyxis trispinoa*

Morphology Larvae of *O. trispinosa* are elongate and slender with mean body depth at the pectoral fin origin of 11.7% SL in preflexion specimens decreasing to 10.7% SL in flexion and postflexion larvae (Tables 2 and 3). Mean head length is 18.4% SL in preflexion larvae and increases to 23.8% SL in juveniles (Table 3). Mean head width is approximately 50.0% HL throughout larval development and decreases to 37.1% HL in juveniles (Table 3). Mean snout length increases from 20.4% HL in preflexion larvae to 27.0% HL in postflexion larvae and eye diameter decreases from 33.3% HL in preflexion larvae to 23.3% HL in juveniles. Mean pectoral-fin length increases from 7.0% SL in preflexion larvae to 19.5% SL in postflexion larvae (Table 3). The gut is moderately long: mean snout to anus distance is 47.9% SL in preflexion larvae and decreases to 33.0% SL in juveniles.

Pigmentation Pigmentation in *O. trispinosa* larvae was relatively consistent among specimens and is a useful distinguishing character (Fig. 5).

Head region Pigmentation on the head of preflexion larvae is present as rows of melanophores on the upper and lower jaws. A few additional melanophores are present on the snout. Melanophores on the opercular and hyoid regions join the upper and lower jaw pigmentation to form a continuous swath giving larvae a "bearded" appearance (Fig. 5A). In flexion larvae, additional melanophores appear posterior to the eye.

Lateral body and gut region The dorsolateral surface of the body above the gut is covered with melanophores with the exception of a patch along the dorsal midline above the pectoral fin. The dorsolateral pigmentation recedes ventrolaterally toward the gut with development and is completely absent in postflexion larvae. Melanophores cover nearly the entire caudal portion of the body in preflexion larvae. In some specimens, the notochord tip is unpigmented. In late flexion and postflexion larvae, pigmentation on the lateral body surface begins to separate gradually into seven bands (Fig. 5D). The first band extends from the posterior region of the first dorsal fin to the ventral body midline immediately posterior to the anus. The second band extends between the first two soft rays of the

Table 1

Head spine terminology in agonid larvae listed by sequence of development in *Odontopyxis trispinosa*. (P) designates dermal plate.

Abbreviation	Spine/Plate name	Bone of origin	Adult spine/plate
PA	Parietal	Parietal	Parietal
SPO	Supraocular	Frontal	Supraocular
SC	Supracleithral	Supracleithrum	Supracleithral
CO	Coronal	Frontal	(Overgrown)
PT	Pterotic	Pterotic	Pterotic
NA	Nasal	Nasal	Nasal
APO-4	4th Anterior Preopercular	Preopercle	(Overgrown)
PPO-1,2	1st, 2nd Posterior Preopercular	Preopercle	Preopercular
PPO-3,4	3rd, 4th Posterior Preopercular	Preopercle	Preopercular
SIO-5,6	5th, 6th Superior Infraorbital	Infraorbital 3	Posterior infraorbitals
CL	Cleithral	Cleithrum	(Overgrown)
TM	Tympanic	Frontal	(Overgrown)
OP	Opercular	Opercle	Opercular
FR	Frontal	Frontal	(Overgrown)
SOP	Subopercular	Subopercle	Gill Cover Spine
SIO-1,2	1st, 2nd Superior Infraorbital	Infraorbital 1 (Lachrymal)	Anterior Infraorbital
PSO-1	1st Postocular	Frontal	Postocular
PSO-2,3	2nd, 3rd Postocular (P)	(Dermal)	Postocular Plates
RO	Rostral	Rostral Plate	Rostral
PST	Posttemporal (P)	(Dermal)	(Overgrown)
IIO-1,2	1st, 2nd Inferior Infraorbital (P)	(Dermal)	Anterior, Medial Cheek Plates
SIO-3,4	3rd, 4th Superior Infraorbital	Infraorbital 2 (Jugal)	Medial Infraorbital
IIO-3	3rd Inferior Infraorbital (P)	(Dermal)	Posterior Cheek Plate
SCL	Sclerotics (P)	Sclerotic	Eyeball Plates

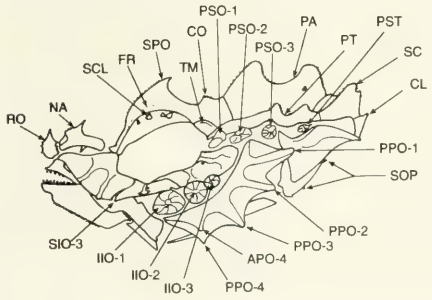

Figure 3

Positions and abbreviations of larval head spines and plates in agonids. Based on a 17.2-mm stained larva of *Odontopyxis trispinosa* (modified from Moser and Ahlstrom (1978), Richardson and Laroche (1979), and Laroche (1986)).

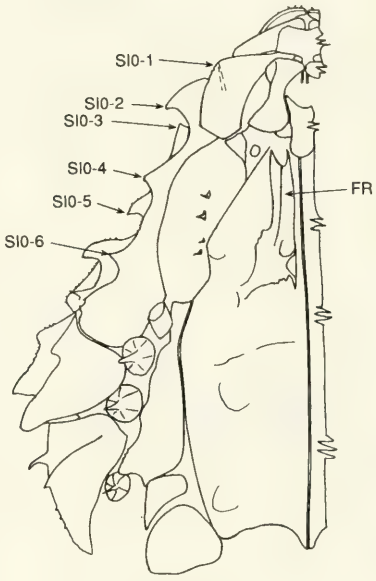

Figure 4

Top view above eye showing superior infraorbital and frontal spines of a 17.2-mm SL, cleared and stained *Odontopyxis trispinosa*.

dorsal and anal fins and is connected ventrally to the first band by a bar. The third band extends from the posterior half of the second dorsal fin to the posterior half of the anal fin. The remaining four bands are evenly spaced on the body between the posterior edges of the second dorsal and anal fins and the caudal fin. The third, fifth, and seventh bands are the widest. The posteriormost band of pigmentation in postflexion larvae and early juveniles is located at the hypural margin and is continuous with the caudal-fin pigment.

The entire ventral and lateral surfaces of the gut in preflexion larvae are covered with pigmentation. A dense row of melanophores is present along the ventral midline from the isthmus to the end of the preanal finfold. The ventral midline pigmentation can be distinguished easily in lateral view through the postflexion stage. In some specimens, a small, circular, unpigmented area is present on the lateral surface of the gut posterior to the pectoral-fin rays.

Fins The base of the pectoral fin is completely covered with melanophores throughout development. Pigmentation is absent from the pectoral-fin blade, rays, and membrane.

Most preflexion and flexion specimens possess a small group of melanophores on the anterior portion of the dorsal finfold near the body margin over the gut (Fig. 5A). This patch migrates posteriorly with development and becomes the pigmentation seen on the first dorsal fin in postflexion larvae and juveniles (Fig. 5, C and D). A larger patch of melanophores is present at approximately midbody which usually extends to the dorsal edge of the finfold in preflexion larvae. This dorsal midbody patch recedes toward the body and splits into two somewhat triangular-shaped patches of pigmentation in flexion larvae. This larger patch of pigmentation is retained on the second dorsal fin in postflexion larvae and juveniles. The finfold patches roughly correspond to body bands on postflexion and juvenile specimens. Three additional triangular-shaped patches of melanophores are present approximately two-thirds of the distance between the anus and notochord tip on the dorsal finfold and form a continuous region of pigment extending to the caudal finfold. The triangular-shaped patches of pigmentation separate in flexion larvae and disappear as the finfold recedes in postflexion larvae.

Table 2

Morphometric measurements (in millimeters) of 45 *Odontopyxis trispinosa* larvae and early juveniles. Specimens between dashed lines (— —) were undergoing notochord flexion.

Standard length	Body depth	Snout to anus length	Head length	Head width	Snout length	Eye diameter	Pectoral fin length
4.3	0.44	2.02	0.78	0.40	0.14	0.28	0.30
4.5	0.60	2.06	0.72	0.52	0.12	0.30	0.30
4.6	0.60	2.24	0.80	0.44	0.18	0.30	0.34
5.2	0.62	2.48	1.02	0.48	0.22	0.32	0.34
5.3	0.60	2.52	0.96	0.46	0.20	0.32	0.44
5.3	0.64	2.60	1.02	0.46	0.18	0.36	0.36
5.9	0.62	2.72	1.04	0.42	0.20	0.34	0.38
6.4	0.74	3.24	1.14	0.44	0.26	0.36	0.34
6.7	0.70	3.24	1.20	0.56	0.22	0.40	0.46
6.8	0.76	3.20	1.26	0.56	0.30	0.40	0.50
6.8	0.82	3.12	1.40	0.62	0.30	0.36	0.50
7.2	0.86	3.48	1.36	0.70	0.30	0.40	0.52
7.1	0.88	3.60	1.38	0.70	0.30	0.40	0.50
7.9	0.66	3.40	1.34	0.66	0.32	0.36	0.60
8.5	0.92	4.12	1.76	0.80	0.50	0.44	0.70
9.1	0.96	4.12	1.50	0.66	0.38	0.42	1.00
9.8	1.00	4.60	2.06	0.92	0.60	0.52	1.40
10.0	1.06	4.40	1.70	1.25	0.41	0.45	1.05
10.8	1.20	5.00	2.36	1.08	0.52	0.60	1.46
11.7	1.36	5.25	2.52	1.20	0.60	0.58	1.64
11.8	1.42	5.50	2.26	1.24	0.74	0.56	2.46
11.8	1.44	5.42	2.80	1.24	0.76	0.60	2.26
12.5	1.22	5.67	2.70	1.20	0.74	0.60	2.08
12.6	1.32	5.83	2.80	1.44	0.86	0.70	2.48
12.7	1.26	5.42	2.76	1.28	0.76	0.64	2.42
12.8	1.30	5.83	2.70	1.20	0.68	0.60	2.42
13.7	1.64	6.33	2.92	1.50	0.90	0.72	2.24
13.8	1.58	6.08	2.92	1.30	0.80	0.66	2.35
13.9	1.38	6.08	3.00	1.46	0.74	0.70	2.80
14.3	1.50	6.17	3.25	1.50	0.80	0.74	2.96
14.7	1.32	5.87	3.00	1.40	0.72	0.76	2.64
14.8	1.52	6.08	3.00	1.40	0.76	0.66	2.68
15.0	1.60	5.83	3.60	1.54	0.90	0.84	3.20
15.2	1.70	5.92	3.84	1.80	1.00	0.84	3.20
15.4	1.66	6.17	3.20	1.60	0.84	0.72	3.20
15.8	1.62	6.63	3.50	1.82	0.91	0.86	3.16
16.7	1.70	6.50	4.24	2.04	1.12	0.98	3.68
17.5	1.87	6.84	4.26	1.98	1.13	0.90	3.08
17.7	2.20	7.58	4.32	1.86	1.24	0.84	3.72
17.7	1.76	7.00	4.48	2.00	1.20	1.06	3.68
28.0	2.75	9.58	7.40	2.88	1.56	1.64	4.68
32.1	3.33	10.50	7.58	2.88	1.84	1.75	5.58
34.8	3.42	11.30	8.08	3.12	1.92	2.00	6.00
36.4	3.92	11.70	8.25	2.92	2.17	1.92	6.33
41.6	4.83	14.50	9.67	3.33	2.50	2.25	6.92

A small patch of melanophores is present on the anal finfold immediately posterior to the anus. This small patch of pigmentation is a useful character which persists until postflexion when it migrates dorsally with the receding finfold to form the bar between the first and second body bands (Fig. 5D). A large triangular-shaped patch of pigment is present at midbody and extends nearly to the finfold margin in preflexion and early flexion larvae. The large triangular-shaped patch expands ventrally to the finfold margin and becomes more rectangular shaped in late flexion larvae. This is the only pigmentation present on the anal fin in postflexion larvae and juveniles (Fig. 5, C and D). Two additional patches of melanophores are present on the anal finfold in preflexion larvae. These form a nearly continuous region of pigmentation which begins at approximately two-thirds of the distance between the anus and notochord tip which extends to the caudal finfold. This pigmentation breaks apart in late flexion larvae and disappears as the finfold recedes in postflexion larvae.

The posteriormost dorsal and anal finfold pigmentation connect and are continuous with a large semicircular patch of melanophores which covers nearly

Table 3

Body proportions of *Odontopyxis trispinosa* larvae and early juveniles. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Preflexion	Flexion	Postflexion	Juvenile
Sample size	12	8	20	5
Standard length	5.7±1.0 (4.3–7.2)	9.4±1.5 (7.1–11.7)	14.5±1.9 (11.8–17.7)	34.6±5.1 (28.0–41.6)
Body depth/SL	11.7±1.0 (10.2–13.4)	10.7±1.2 (8.4–12.4)	10.7±0.9 (9.0–12.4)	10.5±0.7 (9.8–11.6)
Snout to anus length/SL	47.9±1.4 (45.7–50.3)	46.2±2.5 (43.2–50.8)	42.5±2.8 (38.9–46.6)	33.3±1.2 (32.1–34.9)
Head length/SL	18.4±1.2 (16.1–20.5)	19.4±2.2 (16.5–21.8)	22.4±1.9 (19.2–25.4)	23.8±1.5 (22.7–26.4)
Head width/HL	48.7±8.7 (40.4–72.2)	50.1±9.7 (44.0–73.5)	47.2±3.3 (43.1–54.9)	37.1±2.0 (34.4–38.9)
Snout length/HL	20.4±2.3 (16.7–23.8)	24.8±2.7 (21.7–29.1)	27.0±2.3 (24.0–32.7)	24.3±2.1 (21.1–26.3)
Eye diameter/HL	33.3±4.0 (25.7–41.7)	26.1±1.9 (23.0–29.0)	23.0±1.5 (19.4–25.3)	23.3±0.9 (22.2–24.8)
Pectoral fin length/SL	7.0±0.7 (5.3–8.4)	10.8±2.9 (7.1–14.2)	19.5±1.7 (16.3–21.3)	17.1±0.4 (16.6–17.4)

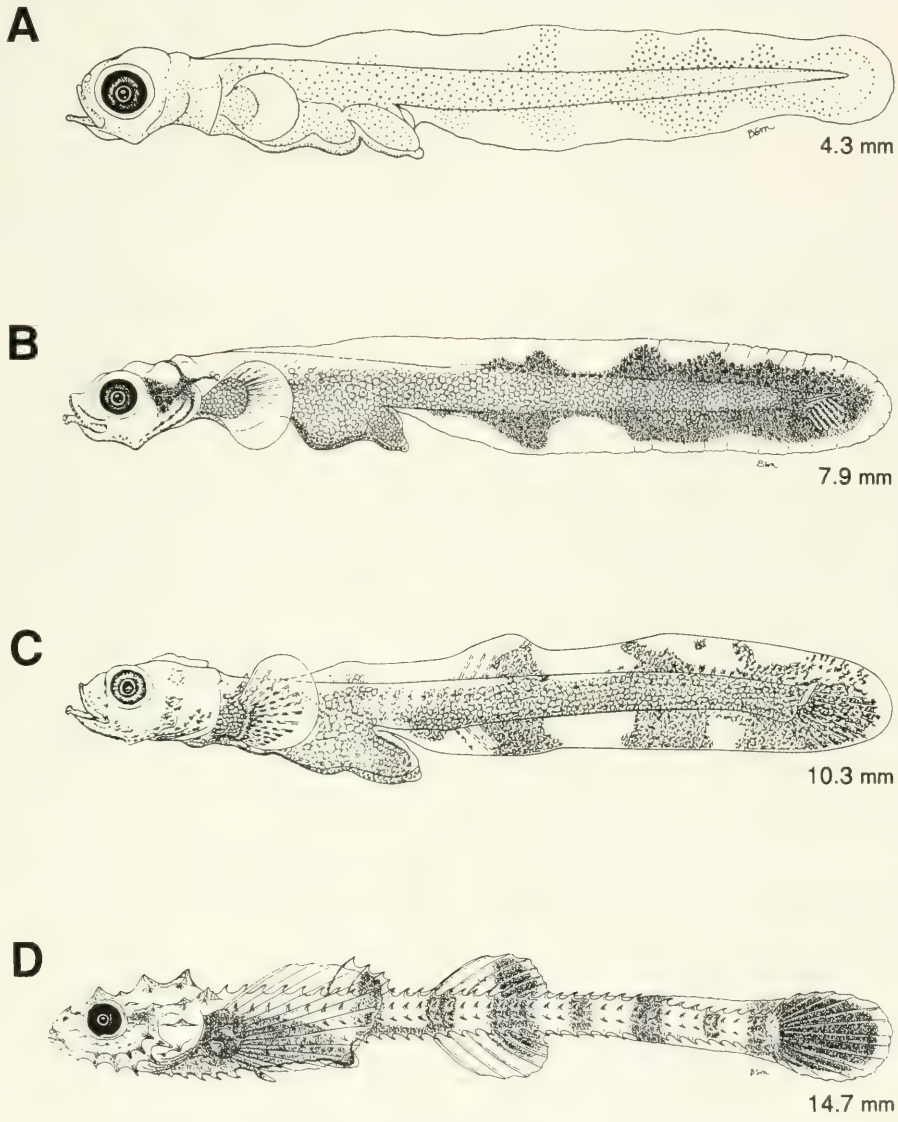

Figure 5

Larval stages of *Odontopyxis trispinosa*. (**A**) Preflexion larva 4.3 mm SL, CalCOFI 5405-73.50. (**B**) Early flexion larva 7.9 mm SL, CalCOFI 6304-110.32. (**C**) Flexion larva 10.3 mm SL, VPA, Lambert Channel 4/26/91 No. 7. (**D**) Postflexion larva 14.7 mm SL, CalCOFI 7412-83.44.

the entire caudal finfold. Caudal pigmentation persists throughout development.

Osteology Although precursors of some bony structures such as dermal plates and fin rays are discernable as early as 8.0 mm, actual ossification of skeletal elements in *O. trispinosa* does not begin until approximately 12.0 mm.

Cranium The parasphenoid and basioccipital bones of the cranium begin to ossify at 11.7 mm. At 13.2 mm, several bones, including the nasal, frontal, parietal, parasphenoid, basioccipital, and exoccipital are completely ossified. The rostral plate, nasal, lateral ethmoid, supraethmoid, vomer, exoccipital, lachrymal, and remainder of the circumorbital series ossify by 14.8 mm. The sphenotic, prootic, epiotic, tabular, and pterosphenoid are ossified by 27.0 mm.

Spines Numerous head spines are ossified at 12.6 mm including the nasal, supraocular, the large bilobed parietal, coronal, pterotics, supracleithral, anterior preoperculars and posterior preoperculars 1 and 2. The tympanic, cleithral, opercular, fifth and sixth superior infraorbital spines, and the third and fourth posterior preopercular spines are also ossified at this stage. The frontal spine forms by 13.8 mm but is not visible in lateral view because it is small and located behind the anterior margin of the supraocular spine. The frontal spine becomes overgrown with bone and is difficult to distinguish at 17.2 mm. Interopercular and superior infraorbital spines 1 and 2 begin forming at about 14.2 mm. The rostral and postocular spines and the postocular and posttemporal plates ossify at 14.8 mm. Superior infraorbital spines 3 and 4 and inferior infraorbital plates 1 and 2 are completely ossified at this size. The third inferior infraorbital and sclerotic plates are ossified by 17.2 mm. All spines described here are paired with the exception of the rostral.

Mandibular region The dentary, angular, and articular bones of the lower jaw are the first to ossify in postflexion larvae of 11.7 mm. At 12.6 mm, the premaxilla and maxilla are ossified.

Palatine region Palatine, quadrate, metapterygoid, mesopterygoid, ectopterygoid, and symplectic bones are ossified at 12.6 mm.

Opercular region The preopercle, opercle, interopercle, and subopercle are ossified by 12.6 mm.

Hyoid region The basihyal, hypohyal, urohyal, ceratohyal, epihyal, interhyal, glossohyal, and branchiostegal rays are also ossified by 12.6 mm. The hyomandibula is ossified by 27.0 mm.

Branchial region The pharyngobranchial teeth are the first structures to ossify by 11.7 mm. Ossification of the pharyngobranchials occurs at about 17.2 mm. The pharyngobranchials begin as four pieces of cartilage that apparently fuse before ossification of the pharyngobranchial teeth. This process, however, was not observed. The epibranchials (n=4) and ceratobranchials (n=5) also ossify by 17.2 mm. The remaining branchial support structures, including the hypobranchials (n=3) and basibranchials (n=3), ossify by 27.0 mm.

Appendicular region The cleithrum, postcleithrum, and coracoid are ossified by 12.6 mm. The pelvic-fin spine and all pectoral-fin rays, with the exception of the ventralmost, ossify by 12.8 mm. The two pelvic-fin rays and the final (14th) pectoral-fin ray are ossified by 13.2 mm. The supracleithrum ossifies at about 13.8 mm. At 14.8 mm, ossification of the posttemporal is completed. Ossification of the basipterygium occurs at 17.2 mm. The scapula and three radials supporting the pectoral-fin rays are ossified by 27.0 mm.

Median fins All dorsal- and anal-fin spines and soft rays are ossified by 12.6 mm (Table 4). Six superior principal rays and five inferior principal rays in the caudal fin are ossified at this size (total=11). One inferior principal (12), and two superior procurrent rays (13, 14) are ossified by 13.2 mm. By 17.2 mm one additional superior (15) procurrent caudal ray is formed which completes the adult count (3+6+6+0=15). Ossification of the epural, hypural plate, and pterygiophores supporting the dorsal- and anal-fin rays is completed by 27.0 mm.

Vertebral column Ossification of vertebral elements progresses from anterior to posterior. Notochord flexion begins at approximately 7.0 mm and is completed by 11.8 mm. All, except the posteriormost caudal vertebral centrum, are ossified by 12.6 mm. The urostyle and the anteriormost neural and haemal spines are also complete by 12.6 mm. All abdominal neural spines are complete and three additional haemal spines form anteriorly by 13.2 mm. All vertebral centra are ossified by 13.8 mm and two additional haemal spines have formed. By 14.2 mm, 22 additional haemal spines develop. All neural spines are ossified by 14.8 mm and haemal spines are complete at 15.4 mm.

Dermal plates Precursors of the supra (SLP) and infralateral (ILP) plates first appear as small singular spines which are distinguishable at about 8.0 mm. Ossification, however, does not begin until approximately 12.0 mm and progresses from anterior to posterior. Bone develops radially from the base of the spine to eventually form the juvenile/adult dermal plate. By 12.6 mm, ossification of the SLP and ILP series is complete. The dorsolateral and mid-dorsal (DLP+MDP) and the ventrolateral and mid-ventral (VLP+MVP) plate series are complete by 14.8 mm. The lateral line (LLP) plate series begins to form at about 14.0 mm. Lateral line plates are the only plates that begin development as bifurcate spines. Ossification of the LLP series is complete

Table 4

Meristics of cleared and stained *Odontopyxis trispinosa* larvae and early juveniles. Specimens between dashed lines (— —) were undergoing notochord flexion.

Standard length (mm)	Dorsal fin		Anal fin	Pectoral fin rays	Pelvic fin spines, rays	Branchiostegal rays	Neural spines			Haemal spines	Centra			Body plates[1]				
	spines	rays	rays				abdominal	caudal	total		abdominal	caudal	total	DLP+MDP	SLP	LLP	ILP	VLP+MVP
5.3																		
5.8																		
6.1																		
7.0																		
7.7																		
8.3																		
8.5																		
9.3																		
10.0																		
11.4																		
11.7																		
12.5																		
12.6	5	6	6	13	I	6	3		3		13	25	38	30	35		35	32
13.1	3	6	2	2														
13.2	5	6	6	14	I,2	6	13	20	33	3	13	27	40	32	38	2	36	34
13.8		3				6	2		2									
13.8	4	6	7	13	I,2	6	13	22	35	6	13	27	40	34	38		36	37
14.2	5	7	6	14	I,2	6	13	19	32	5	13	26	39	34	36	1	35	34
14.8	5	7	6	14	I,2	6	13	25	38	29	13	26	39	36	38	38	37	36
15.2	5	6	6	13	I,2	6	13	25	38	23	13	26	39	37	39	33	37	37
15.2	4	4	6	14	I,2	6	13	25	38	26	13	26	39	37	37	1	35	36
15.4	4	6	7	14	I,2	6	13	24	37	31	13	25	38	36	37	23	36	37
16.7	5	6	6	14	I,2	6	13	25	38	31	13	26	39	37	37	20	35	37
17.2	6	6	7	14	I,2	6	13	25	38	31	13	26	39	37	38	38	36	37
27.0	4	6	5	14	I,2	6	13	25	38	32	13	26	39	36	37	39	36	36
29.0	5	6	6	14	I,2	6	13	24	37	31	13	25	38	37	39	38	36	37
41.0	4	6	6	13	I,2	6	13	24	37	31	13	25	38	36	38	39	36	36

[1] DLP=dorsolateral; MDP=mid-dorsal; SLP=supralateral; LLP=lateral line; ILP=infralateral; VLP=ventrolateral; MVP=mid-ventral.

by 17.2 mm. Breast plates on the ventral surface of the abdomen and pelvic region are complete by 12.6 mm. The number of pectoral-fin base plates in *O. trispinosa* is variable ranging from 3 to 8 among specimens examined. Ossification of pectoral-fin base plates is complete by about 13.8 mm.

Development of *Xeneretmus latifrons*

Morphology Larvae of *X. latifrons* are deeper bodied than *O. trispinosa*; mean body depth at the pectoral-fin origin ranges from 13.3% SL in preflexion specimens to 14.6% SL postflexion (Tables 5 and 6; Fig. 6). Head length increases from 20.3% SL in preflexion larvae to 26.6% SL in postflexion larvae, and snout length as a proportion of head length increases from 18.8% HL in preflexion larvae to 24.4% HL in postflexion larvae (Table 6). Eye diameter decreases from about 37.5% HL in preflexion larvae to 28.4% HL in postflexion larvae, and head width remains approximately 54–55% HL throughout development (Table 6).

Pectoral-fin length increases from 8.4% SL in preflexion larvae to 21.8% SL in postflexion larvae. In preflexion larvae, snout to anus distance is 51.7%

Table 5

Morphometric measurements (in millimeters) of 45 *Xeneretmus latifrons* larvae. Specimens between dashed lines (— —) were undergoing notochord flexion.

Standard length	Body depth	Snout to anus length	Head length	Head width	Snout length	Eye diameter	Pectoral fin length
4.9	0.72	2.20	0.84	0.48	0.06	0.38	0.34
5.1	0.66	2.56	0.96	0.50	0.16	0.38	0.34
5.1	0.70	2.48	1.06	0.54	0.20	0.38	0.38
5.3	0.66	2.40	0.90	0.44	0.16	0.38	0.32
5.5	0.76	2.88	1.26	0.66	0.26	0.40	0.44
5.6	0.68	2.92	1.00	0.50	0.20	0.40	0.40
6.0	0.78	2.92	1.14	0.64	0.23	0.44	0.50
6.0	0.72	2.98	1.15	0.60	0.22	0.40	0.40
6.8	0.82	3.40	1.32	0.66	0.24	0.46	0.42
6.8	0.80	3.36	1.20	0.66	0.20	0.42	0.50
7.0	1.10	3.80	1.66	0.80	0.28	0.46	0.52
7.2	0.88	4.04	1.80	1.00	0.42	0.52	1.08
7.8	1.16	4.80	2.08	1.08	0.56	0.64	1.14
7.9	0.96	4.12	1.54	0.84	0.30	0.48	0.62
8.3	1.30	4.78	1.54	1.13	0.32	0.61	0.81
8.9	1.14	4.78	1.94	1.04	0.44	0.62	0.88
9.3	1.30	5.67	2.68	1.52	0.50	0.82	1.80
9.8	1.18	5.33	2.44	1.24	0.56	0.68	1.50
9.9	1.60	5.50	2.56	1.44	0.64	0.74	1.80
10.0	1.20	6.08	2.44	1.36	0.60	0.74	1.62
10.0	1.48	5.67	2.36	1.30	0.54	0.70	1.42
10.5	1.50	5.75	2.96	1.64	0.62	0.86	2.48
10.8	1.72	6.17	2.68	1.42	0.62	0.80	2.14
10.8	1.72	6.25	2.80	1.80	0.64	0.88	2.32
11.4	1.68	6.50	2.88	1.86	0.72	0.88	2.30
11.8	1.88	6.50	2.88	1.70	0.74	0.78	2.20
11.8	1.64	6.08	2.88	1.90	0.70	0.76	3.00
12.5	1.96	6.67	3.28	1.94	0.78	1.02	2.64
12.7	1.97	7.00	3.44	1.88	0.94	0.86	2.80
12.7	1.96	6.67	3.36	2.06	0.66	0.96	3.00
13.2	2.06	6.70	3.52	2.00	0.90	0.92	3.12
13.9	2.30	7.08	3.92	2.30	0.98	1.02	3.52
14.2	2.10	7.12	4.04	2.10	1.10	1.08	3.72
14.7	2.22	7.58	3.84	2.12	0.94	1.02	3.52
14.7	2.08	7.33	3.56	2.10	0.78	0.96	3.76
15.5	2.58	7.14	3.80	2.58	0.91	1.09	3.73
16.6	2.74	8.06	4.86	2.30	1.06	1.22	4.40
16.8	2.52	7.92	4.60	2.40	1.16	1.26	3.84
18.3	2.58	8.06	4.86	2.74	1.37	1.22	4.10
22.0	3.04	9.40	5.17	3.04	1.67	1.52	4.41
30.0	3.67	11.50	8.67	3.60	2.25	2.25	5.33
30.5	4.00	11.30	8.67	4.33	1.92	2.92	5.50
31.8	3.92	11.80	9.58	4.42	2.00	3.08	5.58
39.2	4.33	12.70	10.70	4.75	2.33	3.42	6.83
42.0	5.12	14.20	11.20	5.42	2.50	3.67	7.08

Table 6

Body proportions of *Xeneretmus latifrons* larvae. Values given for each body proportion are expressed as percentage of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Preflexion	Flexion	Postflexion
Sample size	15	8	22
Standard length	6.3±1.1 (4.9–8.3)	9.9±0.6 (8.9–10.8)	19.0±9.4 (10.8–42.0)
Body depth/SL	13.3±1.4 (11.9–15.7)	14.2±1.6 (12.1–15.9)	14.6±1.6 (11.0–16.6)
Snout to anus length/SL	51.7±4.5 (44.7–61.9)	56.7±2.7 (53.6–60.8)	47.4±7.6 (32.4–57.9)
Head length/SL	20.3±3.0 (17.1–26.8)	25.3±2.3 (21.7–28.7)	26.6±1.8 (23.5–30.1)
Head width/HL	53.9±6.0 (48.2–73.4)	54.8±2.0 (50.8–56.7)	55.6±7.2 (41.5–67.9)
Snout length/HL	18.8±4.2 (7.1–26.9)	22.6±2.0 (18.7–25.0)	24.4±2.8 (19.6–32.3)
Eye diameter/HL	37.5±5.1 (27.7–45.2)	29.8±1.2 (27.9–32.0)	28.4±2.8 (25.0–33.7)
Pectoral fin length/SL	8.4±2.8 (6.1–15.1)	17.1±4.1 (9.9–23.6)	21.8±3.1 (16.9–26.5)

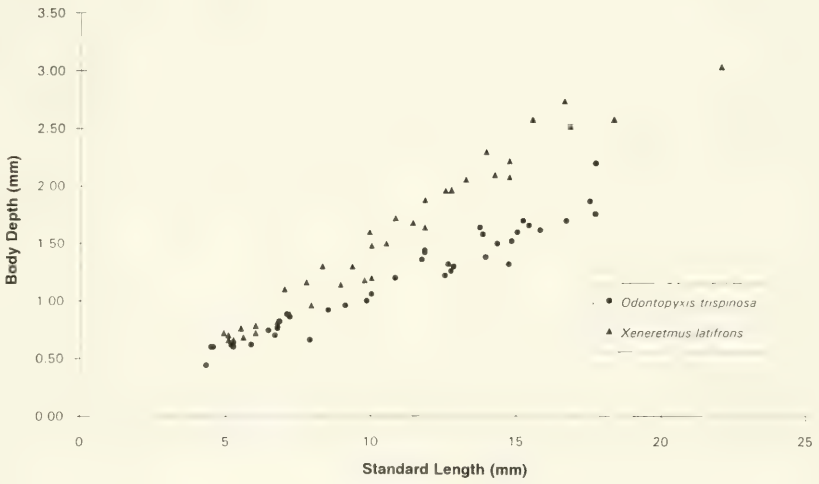

Figure 6
Plot of body depth vs. standard length (mm) for larval *Odontopyxis trispinosa* and *Xeneretmus latifrons*.

SL, increases to 56.7% SL during flexion, and decreases to 47.4% SL during postflexion.

Pigmentation Pigmentation in *X. latifrons* is consistent among specimens and is a useful distinguishing character (Fig. 7). Because pigmentation on the head and gut regions of *X. latifrons* is so similar to that described previously for *O. trispinosa*, discussion here will be limited to areas of the lateral body and fins that are diagnostically important.

Lateral body The lateral surface of the body above the gut in preflexion larvae is covered with melanophores, with the exception of an elongate, unpigmented area along the dorsal midline above the pectoral fin. Melanophores cover nearly the entire caudal region of the body, with the exception of the notochord tip. Melanophores extend along the dorsal and ventral margins of the unpigmented area around the notochord tip (Fig. 7A). By early flexion, melanophores completely cover the notochord tip (Fig. 7B).

Three patches of melanophores appear along the dorsal midline near the notochord tip by about 10.5 mm SL (Fig. 7C). The anterior patch forms the first band which extends from the dorsal margin of the body, posterior to the pectoral-fin base, to the anterior lateral gut area. The second band extends dorsally to connect with pigmentation seen on the first dorsal fin. The third band transverses the body between the posteriormost dorsal spine and the gut. Four or five distinct bands of pigmentation form between the anterior edges of the second dorsal and anal fins and the caudal fin. The first two bands transverse the body between the anterior and posterior margins of the second dorsal and anal fins. One or two bands are present between the posteriormost dorsal- and anal-fin rays and the hypural margin. The last band is the widest and covers the hypural region, extending into the caudal fin approximately 15–20% of its length (Fig. 7, C and D).

Fins Melanophores begin to appear on the ventral margin of pectoral-fin base at about 5.0 mm. The pectoral-fin base is completely covered with pigment by 6.0 mm. Pigmentation is always absent from the pectoral-fin blade, rays, and membrane (Fig. 7, A and B).

A small patch of melanophores appears in the dorsal finfold above the constriction of the gut at about 6.0mm (Fig. 7B). This pigmentation later expands and is that seen on the spinous (first) dorsal fin in late flexion and postflexion larvae (Fig. 7, C and D). Posteriorly, an additional patch of pigmentation begins about one-third of the distance between the anus and notochord tip and exhibits an irregular edge, appearing somewhat serrated, below the dorsal margin.

In preflexion larvae, a large patch of melanophores covers most of the anal finfold beginning at approximately one-fourth of the distance between the anus and notochord tip and continuing its entire length. The rela-

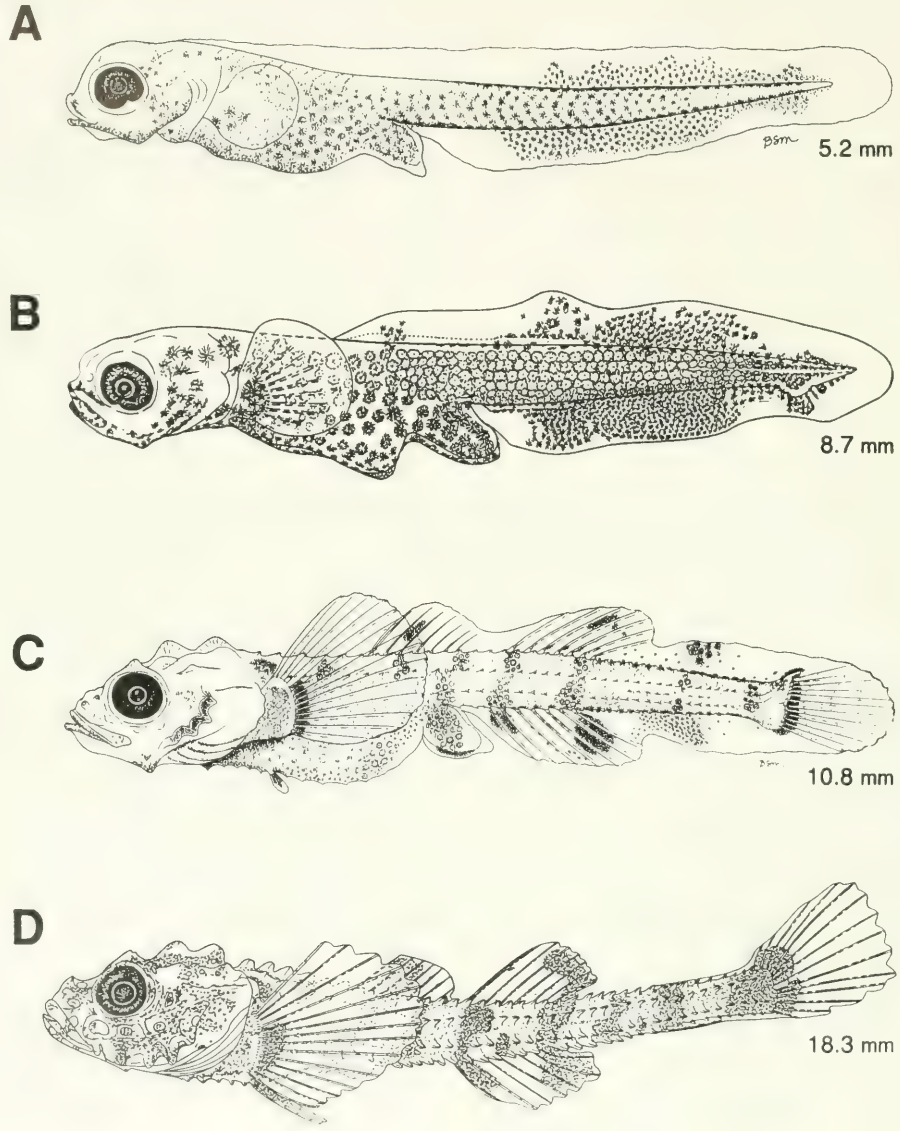

Figure 7

Larval stages of *Xeneretmus latifrons*. (**A**) Preflexion larva 5.2 mm SL, CalCOFI 6501BD-83.43. (**B**) Early flexion larva 8.7 mm SL, VPA, Lambert Channel 4/22/90 No. 5. (**C**) Flexion larva 10.8 mm SL, CalCOFI 5403CR-83.48. (**D**) Postflexion larva 18.3 mm SL, VPA, Lambert Channel 5/3/88 No. 4.

tively large unpigmented area anterior of this patch is an important diagnostic feature (Fig. 7, A and B).

Both the dorsal and ventral finfold melanophore patches are constricted nearly to the body margins at a point about 80%–90% of the distance between the anus and notochord tip (Fig. 7B). As notochord flexion progresses, the ventral patch of pigmentation posterior to the constriction on the anal finfold is seen as the post-hypural pigment present on the caudal fin of postflexion specimens (8.7–22.0 mm)(Fig. 7C). This caudal-fin pigmentation extends posteriorly to about 15–20% of the caudal-fin length (Fig. 7, C and D).

The remaining melanophores on the dorsal and anal finfolds migrate toward the body margins as the finfold recedes. Discrete melanophore patches remain on the anterior and posterior margins of the second dorsal and anal fins in postflexion larvae (Fig. 7D).

Osteology Although precursors of some bony structures such as dermal plates and fin rays are discernable as early as 8.0 mm, ossification in *X. latifrons* does not begin until approximately 13.0 mm. The sequence of ossification of bony structures in *X. latifrons* is nearly identical to that described previously for *O. trispinosa*. The most important difference to note is that ossification in *X. latifrons* begins later (13.0 mm), progresses more rapidly for lateral body plates, and is slower for most skeletal elements than *O. trispinosa*. The intent here is to highlight important differences between the two taxa.

Cranium All parts of the cranium, with the exception of the sphenotic, prootic, epiotic, tabular, and pterosphenoid are ossified at 13.8 mm. These remaining cranial elements ossify at about 30.5 mm.

Mandibular region Ossification of all mandibular structures is complete at 13.8 mm.

Spines Head spination is generally reduced in *X. latifrons* larvae. *Xeneretmus latifrons* larvae have no inferior infraorbital, postocular, or posttemporal plates and have only four superior infraorbital spines. The rostral spine, which is weaker than that of *O. trispinosa*, and sclerotic plates do not develop until the late postflexion stage (about 25–30 mm). The tympanic and frontal spines are more pronounced in *X. latifrons* larvae than in *O. trispinosa*.

Palatine region The palatine, quadrate, metapterygoid, mesopterygoid, ectopterygoid, and symplectic are ossified at 13.8 mm.

Opercular region The preopercle, opercle, subopercle, and interopercle are ossified by 13.8 mm.

Hyoid region The basihyal, hypohyal, urohyal, ceratohyal, epihyal, interhyal, glossohyal, and branchiostegal rays are ossified by 13.8 mm. The hyomandibula is ossified at 30.5 mm.

Branchial region The pharyngobranchial teeth, pharyngobranchials (n=4, fused as in *O. trispinosa*), ceratobranchials (n=5), and epibranchials (n=4) ossify at about 21.0 mm. The remainder of the branchial apparatus including the basibranchials (n=3) and hypobranchials (n=3), are ossified by 30.5 mm.

Appendicular region The cleithrum, postcleithrum, supracleithrum, and coracoid are ossified by 13.8 mm. Pelvic-fin spines and rays and all pectoral-fin rays are complete at 13.8 mm (Table 7). The basipterygium and posttemporal ossify by 21.0 mm. The scapula and three radials supporting the pectoral fin are ossified by 30.5 mm.

Median fins All dorsal-, anal-, and caudal-fin spines and soft rays are ossified by 13.8 mm (Table 7). The caudal fin has 6 superior principal, 2 superior procurrent, 6 inferior principal, and 1 inferior procurrent rays (2+6+6+1=15 total). Ossification of the hypural plate and the pterygiophores supporting the dorsal- and anal-fin rays was not complete in the largest specimen examined (39.2 mm).

Vertebral column Notochord flexion begins at approximately 8.5 mm and is completed by 11.0 mm. All vertebral centra and the urostyle are ossified by 13.8 mm. All except the two posteriormost neural and three haemal spines are also ossified at 13.8 mm. Ossification of all neural and haemal spines is complete by 14.5 mm (Table 7).

Dermal plates All dermal plates are ossified by 13.8 mm. Sequence and direction of formation and ossification is the same as previously described for *O. trispinosa*. *Xeneretmus latifrons*, however, has higher DLP+MDP, ILP, and VLP+MVP lateral body plate series counts than *O. trispinosa* (Tables 4 and 7). A maximum of five pectoral-fin plates was counted in *X. latifrons*.

Discussion

Summary comparison of *O. trispinosa* and *X. latifrons* larvae

Larvae of *O. trispinosa* and *X. latifrons* can be distinguished by pigmentation, morphological, and meristic characters.

Larvae of *O. trispinosa* possess a semicircular patch of melanophores that nearly covers the entire caudal finfold. This character is diagnostic and present throughout development. The caudal finfold of preflexion *X. latifrons* lacks pigmentation except for a patch located near the ventral margin of the notochord tip. This patch becomes elongate as notochord flexion progresses and becomes a band at the hypural margin. This band extends onto the caudal fin and may cover as much as 20% of its anterior surface.

Preflexion larvae of *O. trispinosa* possess a small patch of melanophores on the anal finfold immediately posterior to the origin, *X. latifrons* larvae have a large

Table 7

Meristics of cleared and stained *Xeneretmus latifrons* larvae. Specimens between dashed lines were undergoing notochord flexion.

Standard length (mm)	Dorsal fin spines	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin spines, rays	Branchiostegal rays	Neural spines abdominal	Neural spines caudal	Neural spines total	Haemal spines	Centra abdominal	Centra caudal	Centra total	Body plates* DLP+MDP	Body plates* SLP	Body plates* LLP	Body plates* ILP	Body plates* VLP+MVP
7.4																		
8.7																		
9.5																		
10.2																		
11.9																		
12.3																		
13.8	7	7	7	15	I,2	6	14	25	39	33	14	28	42	38	38	38	38	38
14.5	6	7	7	14	I,2	6	14	27	41	34	14	28	42	38	38	38	38	38
21.0	7	6	7	14	I,2	6	15	26	41	35	15	27	42	41	41	41	40	41
30.5	7	7	7	15	I,2	6	15	25	40	33	15	26	41	38	38	40	38	38
31.8	7	7	7	14	I,2	6	15	25	40	34	15	26	41	38	38	42	38	38
39.2	6	6	7	14	I,2	6	15	26	41	34	15	26	41	38	38	40	38	38

*DLP=dorsalateral; MDP=mid-dorsal; SLP=supralateral; LLP=lateral line; ILP=infralateral; VLP=ventrolateral; MVP=mid-ventral.

unpigmented region. Flexion and postflexion larvae of *O. trispinosa* possess a single patch of melanophores on the anal fin, *X. latifrons* have two.

Notochord flexion of *O. trispinosa* begins at approximately 7.0mm and is completed by 11.8 mm. The largest planktonic specimens of *O. trispinosa* collected were 17.7 mm. Settlement probably occurs at approximately this size. Notochord flexion of *X. latifrons* begins at approximately 8.5 mm and is completed by 11.0 mm. The largest planktonic specimens of *X. latifrons* collected were 22.0 mm.

Xeneretmus latifrons larvae are deeper bodied than *O. trispinosa*. *Xeneretmus latifrons* also has a wider head than *O. trispinosa* at all stages of development. Single barbels are present at the corners of the mouth at about 15.0 mm in *O. trispinosa* and 18.0 mm in *X. latifrons*. A distinct heart-shaped occipital pit is present in *O. trispinosa* after about 15.0 mm. Postflexion larvae of each taxon are also distinguishable by adult meristic characters.

Ossification of most skeletal elements in *O. trispinosa* begins earlier and is completed at smaller sizes than in *X. latifrons*. Head spination in *X. latifrons* is generally reduced and dermal plates are absent on the head region. The caudal-fin ray complement in *X. latifrons* (2+6+6+1) is notably different than in *O. trispinosa* (3+6+6+0). Ossification of the pterygiophores supporting the dorsal and anal fins, and the hypural plate is complete by 27.0 mm in *O. trispinosa*, but was not evident in cleared-and-stained specimens of *X. latifrons* examined in this study (up to 39.2 mm). This indicates that transformation from larval to juvenile stages in *X. latifrons* occurs at much larger sizes than in *O. trispinosa*. Ossification of dermal body plates occurs in nearly identical sequence, but *X. latifrons* has more plates in the DL+MD, IL, and VL+MV series. Dermal plate formation in *X. latifrons* is complete at a slightly smaller size than in *O. trispinosa*.

The preceding descriptions eliminate the confusion in the literature concerning these larvae which resulted from previous misidentifications (page 463 of Matarese et al. (1989) and Figures A, B, and D from Marliave (1975) are larvae of *O. trispinosa* misidentified as *X. latifrons*; Figure C from Washington et al. (1984) is *X. latifrons*).

Comparison of *O. trispinosa* and *X. latifrons* larvae with other known larval agonids

Presently, larvae of 12 of 25 agonid taxa occurring in the northeastern Pacific Ocean can be identified based on single illustrations or complete developmental descriptions. Of these 12 taxa, only *O. trispinosa* and *X. latifrons* described here are complete, illustrated at all stages of development and include discussions of ossification sequence.

By using body morphology, pigmentation, and meristic characters, larvae of *O. trispinosa* and *X. latifrons* are distinguishable from other northeastern Pacific

Table 8

Summary of characters useful in identifying larval and juvenile agonids from the northeastern Pacific Ocean.*

	Characters					
Species	Body depth	Pectoral fin length	Pigmentation	Number of dorsal fins	Pectoral fin rays	Vertebrae
Aspidophoroides monopterygius	Slender	Elongate	Light	1	9–10	51–53
Bothragonus swanii	Deep	Normal	Moderate	2	10–12	29–31
Chesnonia verrucosa	Moderate	Elongate	Light	2	14–15	34–38
Hypsagonus mozinoi	Deep	Normal	Heavy	2	11–12	34
H. quadricornis	Deep	Normal	Heavy	2	12–14	36
Leptagonus leptorhynchus	Moderate	Normal	Heavy	2	13–15	42–44
Ocella dodecaedron	Moderate	Normal	Light	2	14–16	38–39
Odontopyxis trispinosa	Moderate	Normal	Moderate	2	13–15	37–42
Percis japonicus	Deep	Normal	Heavy	2	12	40.42
Stellerina xyosterna	Moderate	Elongate	Light	2	17–19	34–37
Ulcina olriki	Slender	Elongate	Moderate	1	13–16	38–40
Xeneretmus latifrons	Moderate	Normal	Moderate	2	13–15	39–43

*Sources: Illustrations of *A. monopterygius*, *C. verrucosa*, *H. quadricornis* and *S. xyosterna* are from Washington et al. (1984); *B. swanii* is from Marliave (1975); *H. mozinoi* is from Matarese et al. (1989); *L. leptorhynchus*, *O. dodecaedron*, and *P. japonicus* are from Maeda and Amaoka (1988); *U. olriki* is from Dunbar (1947). Pectoral-fin ray and vertebral counts are from Matarese et al. (1989), with the exception of *H. mozinoi* and the lower count for *P. japonicus* which are from Kanayama (1991).

agonid larvae for which published illustrations are available. (Table 8). Larvae of *Hypsagonus mozinoi*, *H. quadricornis*, and *Percis japonicus* are deeper bodied, have notably shorter snout to first dorsal fin distances, are more heavily pigmented, and have lower vertebral and dermal plate counts than *O. trispinosa* and *X. latifrons* (Washington et al., 1984; Maeda and Amaoka, 1988; Matarese et al., 1989). *Bothragonus swanii* larvae have a very similar body morphology to *H. mozinoi*, *H. quadricornis*, and *P. japonicus* but have considerably less pigmentation (Marliave, 1975).

Larvae of *Chesnonia verrucosa* and *Stellerina xyosterna* have similar body morphologies to *O. trispinosa* and *X. latifrons* but have notably larger pectoral fins with bands of pigmentation on or near their posterior edges (Washington et al., 1984; Matarese et al., 1989). *Ocella dodecaedron* and *Leptagonus leptorhynchus* larvae have a similar body morphology to *X. latifrons*. However, pigmentation of *O. dodecaedron* is more sparse and that of *L. leptorhynchus* is heavier (Maeda and Amaoka, 1988).

Larvae of *Ulcina olriki* are distinguished from *O. trispinosa* and *X. latifrons* by having larger pectoral fins with pigmented edges and only a single dorsal fin (Dunbar, 1947). Larvae of *Aspidophoroides monopterygius* (= *A. bartoni*) have extremely slender bodies, a long pectoral fin with a low fin-ray count, higher vertebral and body plate counts, and a single dorsal fin (Maeda and Amaoka, 1988; Matarese et al., 1989). Studies such as this and others planned for the future are the first steps for providing diagnostic information necessary to accurately identify early life history stages of this interesting family of fishes.

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Modeling the potential of fishery reserves for managing Pacific coral reef fishes

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Abstract.—The potential use of marine fishery reserves (MFRs) for managing fisheries on tropical Pacific coral reefs was assessed with an extension of the Beverton-Holt model. The effects of year-round fishery closures on harvests in adjacent, exploited areas were evaluated. Potential changes in spawning stock biomass per recruit (SSB/R) and yield per recruit (Y/R), when varying fractions of exploitable reef area were closed to fishing, were estimated from published data, approximated natural and fishing mortality rates, size- and maturity-at-age distributions, and "transfer" (emigration and immigration) rates. For select cases, fundamental transfer rates were adjusted for possible density-dependent emigration from closed areas as relative densities decreased in surrounding non-closed areas because of continued fishing. Three hypothetical "fish types" were constructed, bracketing the likely extremes in fundamental transfer rates and related life-history parameters of Pacific coral reef fishes: a small-bodied, fast-growing and short-lived, strongly philopatric species of damselfish was contrasted with a large-bodied, relatively slow-growing, long-lived, vagile species of jack. A "surgeonfish" type was used to represent intermediate parameter values.

Simulations corroborate previous observations that MFRs contribute little, if anything, towards increasing Y/R. Results for the highly vagile jack confirm that rapid transfer rates will negate potential gains in SSB/R resulting from closures. At the opposite extreme, small reef philopatriots like damselfishes would almost never be harvested, because of negligible transfer rates, unless the MFR was periodically opened to fishing. The simulations suggest that the SSB/R of the surgeonfish type is the most likely to benefit from MFRs, because moderate vagility allows biomass to accumulate within the closure despite harvesting in the non-closed area. Results further suggest that growth rate, fishing effort in the non-closed (open) area, natural mortality, and maturity and harvesting schedules importantly influence the potential of MFRs to augment SSB when transfer rates are low to moderate.

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Marine fishery reserves (MFRs), areas closed to harvesting and adjacent to fished areas, have recently been touted as enforceable and cost-effective alternatives to conventional fisheries management measures such as size and bag limits, closed seasons, and limited entry (Davis, 1989; Plan Development Team 1990; Polacheck, 1990; Bohnsack, in press; Davis et al.[1]; Russ et al., in press). MFRs are recognized worldwide as providing sanctuaries in which local populations of desirable species can increase in abundance or attain larger body sizes (McCormick and Choat, 1987; Alcala, 1988; Buxton and Smale, 1989; Clark et al., 1989; Russ 1985, 1989; Alcala and Russ, 1990; Cole et al., 1990; Bennett and Attwood, 1991). In contrast, harvesting is known to alter the abundance and body size distributions (Craik, 1981; Katnik, 1982; Koslow et al., 1988; Plan Development Team 1990) and assemblage structure (Bell, 1983; Russ and Alcala, 1989) of fishes on coral reefs and other localized regions of fishery exploitation.

By providing havens from exploitation within which organisms can attain large adult body sizes, designated refuges protect the most valuable segments of spawning stocks (Plan Development Team, 1990). For most marine organisms with lengthy (≥2 wk-long) planktonic larval stages, MFRs can function as sources of benthic recruits to exploited, often distant, sink populations. The subsequent contribution of these recruits to the fishery might counteract (or forestall) the effects of recruitment overfishing (Carr and Reed, in press; Russ et al., in press). Through the directed movements of settled stages, MFRs might also augment the standing biomass of stocks, including spawning adults, in exploited areas adjacent to MFRs as well as within the MFRs themselves (Polacheck, 1990; Roberts and Polunin, 1991). MFRs thus might provide a management tool that addresses growth overfishing, particularly for multispecies fisheries on tropical coral reefs where conventional management is ineffective (Roberts and Polunin, 1991).

Despite the recognized importance of MFRs as sanctuaries for conserving biomass, their contribution to fishery stocks and yields in adjacent exploited areas is poorly understood (Davis, 1989; Polacheck, 1990; Roberts and Polunin, 1991; Russ et al., in press). An introduction to the problem is provided by Polacheck (1990), who expands the Beverton-Holt equation (Beverton and Holt, 1957) describing the effects of a year-round refuge on the spawning stock biomass (SSB) and yield of a cohort in a surrounding exploited area. Although areal closures on coral reefs are one identified application, Polacheck's (1990, Table 1) simulations use empirical data on the growth, matu-

[1] Davis, G. E., S. C. Jameson, and J. E. Dugan. Potential benefits of harvest refugia in Channel Islands National Park and Channel Islands Marine Sanctuary. Unpubl. manuscr., 25 p. U.S. Natl. Park Service, Channel Islands National Park, CA 93001.

rity, and harvesting schedules of Georges Bank cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. The growth and mortality dynamics of tropical coral reef fishes, however, may be quite unlike those of higher-latitude species (Munro and Williams, 1985; Longhurst and Pauly, 1987). Further simulations using growth and mortality data of other fishes are needed.

Observations of traditional practices by marine islanders (Johannes, 1978) suggest that reserves can augment the *SSB*, and perhaps the yield of tropical reef fishes. To date, controlled empirical measurements of fishery yields in an area adjacent to a MFR have been published for only one study site (Sumilon Island, central Philippines; Alcala and Russ, 1990). The changes in catches that Alcala and Russ (1990) observed, however, were based on yield, not yield per recruit (Y/R), over a 1-year period and therefore may not have represented equilibrium conditions.

The present paper evaluates the effects of permanently closed MFRs of different sizes on net changes in *SSB* and yield for several types of tropical Pacific reef fishes. The author simulated various combinations of fishing mortality and emigration-immigration ("transfer") rates for fishes having different but typical natural growth and mortality schedules. Because tropical reef fishes have higher natural growth and death rates than do temperate zone fishes, the focus is on the relative sensitivity of spawning stock biomass per recruit (SSB/R) and Y/R to MFR size, transfer rates, variations in natural mortality and growth, fishing effort, and age at first capture. Another objective is to compare the management potential of "single large or several small" (SLOSS) (Simberloff, 1988) reserves of equal total area. Finally, the potential of MFRs on island reefs is discussed, with particular reference to reef areas surrounding the island of Oahu, Hawaii.

Methods

Parameter values for von Bertalanffy growth rates, derived mortality rates, and maturity and harvesting schedules were chosen to bracket the spectrum of life histories and exploitation characteristics of tropical Pacific reef fishes. At one extreme, values were assembled to describe a reef transient (e.g., a jack of the family Carangidae) that is relatively slow-growing but long-lived and large-bodied is likely to travel rapidly over relatively large distances. Such species often support valuable commercial fisheries. Values used for growth and mortality rates of the jack resemble those of many species of commercially important snappers, groupers, and jacks from the South Pacific and other tropical seas (Munro, 1983; Munro and Williams, 1985).

A short-lived, fast-growing but small-bodied reef damselfish (family Pomacentridae), with limited movements after settlement, was used to represent the opposite extreme. Such small tropical reef species are collected for the aquarium fish trade.

In between these two extremes lies a broad continuum of fishes with intermediate longevities, body sizes, and movement rates. These fishes probably represent most species targeted by recreational and artisanal fisheries on tropical reefs. The few data available (Galzin, 1987; Ralston and Williams[2]; Russ and St. John, 1988; Dalzell, 1989) suggested a range of moderate growth and mortality rates for a number of Pacific parrotfishes (family Scaridae) and surgeonfishes (family Acanthuridae). For convenience, these fishes were labeled the "surgeonfish" type.

The growth parameters used in this study were based partly on published values for a particular species population, complemented by data for other Pacific populations of the same species. For the pomacentrid, the author used a Moorean population of *Stegastes nigricans* (Galzin, 1987). He selected *Ctenochaetus striatus* as the surgeonfish; the length-weight relation was based on a Moorean population (Galzin, 1987), and a Samoan population provided the VBGF parameters (Ralston and Williams, 1988). Sudekum et al.'s (1991) data for NWHI *Caranx ignobilis* were used to represent the jack. Thus the degree to which values were population-specific varied among the three fish types. Natural mortality rates (M) were estimated using Pauly's (1980) multiple regression of M on maximum size, growth coefficient, and mean water temperature (Pauly and Ingles, 1981); 25°C was chosen as representative for shallow, tropical Pacific waters. All parameter values used are listed by fish type in Tables 1 and 2.

Modeling closure effects

Polacheck's (1990) model of the effects of closure size (1–50%), rates of fish transfer between closed and exploited areas, and fishing mortality rate on the biomass and production of fishes in an adjacent exploited area was used with one small but important difference: the use of a three- rather than a four-sided closed area. (Closures on island reefs usually extend seaward from the shoreline, so fishes can move across upcoast, downcoast, and offshore boundaries only. Other factors being equal, dispersion rates out of and into shore-

[2]Ralston, S., and H. A. Williams. 1988. Age and growth of *Lutjanus kasmira, Lethrinus rubrioperculatus, Acanthurus lineatus,* and *Ctenochaetus striatus* from American Samoa. Dep. of Commer., Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. H-88-18, 11 p.

Table 1

Length-weight relations, von Bertalanffy growth function parameters, and natural mortality rates used to simulate spawning stock biomass per recruit and yield per recruit contour surfaces for damselfish (based on Moorean *Stegastes nigricans* from Galzin, 1987); surgeonfish (length-weight relation: Moorean *Ctenochaetus striatus* from Galzin, 1987; VBGF parameters: Samoan *C. striatus* from Ralston and Williams[2]); and jack (NWHI *Caranx ignobilis* from Sudekum et al., 1991). *M* values were estimated after Pauly (1980) and Pauly and Ingles (1981; see Methods).

Variable	Damselfish	Surgeonfish	Jack
Length-weight relation (Total Length/g)	$W = 0.0195L^{3.0}$	$W = 0.0111L^{3.10}$	$W = 0.0072L^{2.98}$
L_∞ (Total Length, cm)	17.5	28.2	217
W_∞ (g)	128.9	348.6	120,139
K (1/year)	0.374	0.447	0.111
t_0 (year)	–0.042	–0.760	–0.097
M (1/year)	1.5	1.0	0.2

Table 2

Age-specific parameters used to simulate the standing stock and catch (yield) values for each of the reef fish types described in Table 1.

Fish type	Age (yr)	Mean weight[1] (g)	Percent mature[2]	Partial recruitment[3]
Damselfish	1.0	4.77	100	1.00
	2.0	32.40	100	1.00
	3.0	72.20	100	1.00
Surgeonfish	1.0	40.81	0	0
	2.0	101.87	100	1.00
	3.0	164.43	100	1.00
	4.0	217.18	100	1.00
	5.0	257.24	100	1.00
Jack	1.0	110.0	0	0
	2.0	861.7	0	0
	3.0	2587.0	0	0
	4.0	5348.6	100	1.00
	5.0	9061.8	100	1.00
	6.0	13,569.6	100	1.00
	7.0	18,688.4	100	1.00
	8.0	24,235.1	100	1.00
	9.0	30,042.0	100	1.00
	10.0	35,963.5	100	1.00
	11.0	41,878.8	100	1.00
	12.0	47,691.4	100	1.00
	13.0	53,327.1	100	1.00
	14.0	58,731.1	100	1.00
	15.0	63,865.3	100	1.00

[1]Based on mean weight-at-age estimated from weight-specific VBGF; see Table 1 for sources.

[2]Sexual maturity assumed 100% complete at age corresponding to the asymptote of the Von Bertalanffy growth function curve; all fish were assumed immature prior to this age.

[3]All species were defined as fully recruited to the fishery at the age of 100% sexual maturity, no fish entering the fishery prior to that age: Age-at-first-capture, A_c = 1.0, 2.0, and 4.0 years for the damselfish, surgeonfish, and jack, respectively.

line-bounded reef closures will be one-fourth slower than the respective rates for completely nested closures of equal areal extent.)

Polacheck's modified Equation 8 was

$$T_{12} = 3 \cdot T_{1s} \cdot (R_1 / R_s)^{1/2}; \quad (1)$$

where T_{12} is the instantaneous emigration rate from closed area 1 to exploited area 2; T_{1s} is the emigration rate from a closure of R_s standard size; and R_1 is the fractional closure size evaluated. As in Polacheck (1990), the initial fish densities were assumed homogeneous in both areas, and thus the number of fish initially present in area 1 at time t was defined as

$$N_{1,t} = R_1 \cdot N_{total,t} \quad (2)$$

where $N_{total,t}$ = number of individuals in the cohort entering areas 1 and 2 at time t. T_{1s} was allowed to vary among fish types, as types surely differ in their fundamental emigration and immigration rates. Selected values of T_{1s} spanned realistic values for each fish type (damselfish: 0.001, 0.01, and 0.1; surgeonfish: 0.1, 0.25, and 0.5; jack: 0.1, 0.5, and 1.0). T_{21}, the rate of immigration into area 1 from area 2, given the type-specific value of T_{1s}, was as defined by Polacheck (1990, Equation 6).

A basic assumption of the model is that fishing does not affect fish distributions by altering habitat or by promoting density gradients between areas 1 and 2, i.e., dispersal is random and uniform throughout both areas and across their boundaries (Polacheck, 1990). This is realistic for fishes like jacks that range widely or that have very large home ranges. However, the assumption of uniform dispersal throughout both areas is debatable for fishes with home ranges that are small relative to the size of MFRs, particularly for strongly site-attached, territorial species like damselfishes whose ambits are trivial compared to the area of a reserve. Transfer rates that functionally approximate those based on an assumption of uniform, random dispersal might be tenable for home-ranging (or even territorial) organisms, if emigration out of MFRs into adjacent fished areas followed a "stepping stone" pattern with minimal time lags. Limited field data at present both support (Walsh, 1984) and counter (Wellington and Victor, 1988) such a model. The key factors here are the magnitude of time lags and the relative sizes of individual home ranges within particular MFRs.

An R_c value of 0.10 was used to represent the "standard-size" closure (Polacheck, 1990). Fishing mortality rates (F_c) were input over the range from 0.1 to $\geq 3M$, with special evaluation of $F_c = 0.5M$, M, and $2M$, based on the best estimate of natural mortality for each fish type. Total fishing effort (F_2) was homogeneously redistributed throughout the exploited area and fixed in magnitude (at a given F_c), regardless of the size of the closed area (Equation 7 in Polacheck, 1990).

SSB/R and Y/R are used as the primary bases of evaluation. Although measures of biomass are not usually applicable to species like the damselfish that are harvested on a numerical basis (see Ingles and Pauly [1984] for examples of consumptive exploitation of small-bodied fishes in artisanal fisheries), these measures were evaluated in the same way to maintain consistency.

First, the SSB and yield of a cohort were calculated, by using Polacheck's (1990) Equations 2 and 3 for the numerical standing stock and the numerical catch of each cohort comprising that stock:

$$\sum_{(t=1)}^{n} (N_{1,t+1} \cdot \bar{W}_{t+1} \cdot \%\mathrm{mat}_{t+1}), \tag{3}$$

$$\sum_{(t=1)}^{n} (N_{2,t+1} \cdot \bar{W}_{t+1} \cdot \%\mathrm{mat}_{t+1}), \text{ and} \tag{4}$$

$$\sum_{(t=1)}^{n} (C_{2,t} \cdot \bar{W}_t); \tag{5}$$

where $N_{1,t+1}$ and $N_{2,t+1}$ are the numbers of a cohort surviving in the respective area at time $(t+1)$; $C_{2,t}$ is the numerical catch of a cohort in area 2 at time t; $\bar{W}_t$ and $\bar{W}_{t+1}$ represent the mean weights of individual fish of the cohort at times t and $(t+1)$, respectively; and $\%\mathrm{mat}_{t+1}$ is the percentage of the cohort that is sexually mature at time $(t+1)$.

SSB/R and Y/R were then calculated by standardizing the total spawning biomass and yield, respectively, of the cohort over its life span by the total number of recruits potentially (area 1) and directly (area 2) entering the fishery from that cohort (Gabriel et al., 1989). SSB/R was evaluated in terms of percentage of the virgin stock biomass possible if fishing was disallowed in both areas (Polacheck, 1990); 20% of virgin biomass was considered the threshold for recruitment overfishing (Beddington and Cooke, 1983).

Two series of simulations were run. One series treated the T_{12} and T_{21} values as fixed, assuming that, analogous to Polacheck's (1990) analyses for Georges Bank cod, transfer rates would remain constant and independent of relative fish densities in the two areas. Additional simulations, using the same initial T_{1s} values, were run for selected cases; in these runs, subsequent values of the transfer rates were treated as a density-dependent function of the changing, relative fish densities in the two areas. Subsequent values of T_{12} and T_{21} were adjusted as follows:

$$T_{12,t+1} = T_{12,t} \cdot \{(N_{1,t}/N_1)/(N_{2,t}/N_2)\}^x, \text{ and} \tag{6}$$

$$T_{21,t+1} = T_{21,t} \cdot \{(N_{2,t}/N_2)/(N_{1,t}/N_1)\}^x; \tag{7}$$

where N_1 is defined in Equation 2 and N_2 is the initial number of the cohort present in area 2; $N_{1,t}$ and $N_{2,t}$ are the numbers of fish surviving in the respective area at subsequent age t; and x is the power used to scale the ratio of fish densities. In Equations 6 and 7, the ratio of the numbers of fish surviving at time t was further adjusted by the ratio of initial densities in the two areas in order to scale for the propensity to emigrate at the onset. Two values of x were evaluated: 0.125 (eighth root) and 0.5 (square root). (Note: When x equals 0, the T_{12} and T_{21} are fixed; when x equals 1.0, these rates are continually readjusted by the changing ratio of relative densities.) Exponents of 0.125 and 0.5 were chosen because they bracketed rate changes of reasonable magnitude. In the surgeonfish, for example, an eighth-root adjustment would initially accelerate a median T_{1s} of 0.25 by about 20% for a median closure size of 25%, at an F_c of 1.0. The corresponding rate increase due to a square-root adjustment would be 60%.

Inclusion of a term for the density-dependent adjustment of transfer rates, as stocks are fished-down in the non-closed area, extends Polacheck's (1990) evaluation. This is perhaps an unnecessary refinement for stocks such as Georges Bank cod for which harvesting by trawl might reduce habitat quality in the non-closed area (Polacheck, 1990). However, non-destructive (e.g., hook and line) methods of artisanal fisheries on coral reefs do not reduce habitat quality. Furthermore, fishes may emigrate at an accelerated rate from a closure into the surrounding non-closed area where densities continue to decrease (tantamount to improving habitat quality). Compensatory emigration resulting from a density gradient is recognized as potentially important in the siting and design of nature reserves (Schonewald-Cox and Bayless, 1986).

Complementary simulations

In addition, the effects of varying M and the age-at-first capture (A_c) on total biomass per recruit (B/R) were simulated with the conventional Y/R model of Beverton-Holt (Sparre et al., 1989). Fishing mortality was evaluated at $0.5M$, M, and $1.5M$ or $2M$. A_c was

examined with the most reasonable estimate of $A_c \pm 50\%$ for each of the three fish types (see footnote C of Table 2 for the type-specific values of A_c used in modeling closure effects). An age-at-recruitment to fishery habitat (A_r) value of 1.0 year was assumed for the surgeonfish and jack, and an A_r of 0.5 year for the damselfish.

Results

General

Results corroborate several of Polacheck's (1990) major results: SSB/R increased, while Y/R generally decreased, with increasing refuge size (Fig. 1). Even in cases where a closure positively affected yield, Y/R increased little. Y/R often was greater at higher levels of fishing effort (Fig. 1) and usually decreased at larger refuge sizes; the rate of decrease was less at higher fundamental transfer rates (Fig. 2, A–C). SSB/R was generally greater for closures of larger size at any particular transfer rate (Figs. 1 and 2). The positive effects of a closure of a given size on SSB/R were greater at lower rates of exploitation and diminished at higher transfer rates (Fig. 3). The rate of increase in SSB/R with refuge size was greater at lower transfer rates (Fig. 1, A–C). The progressive gain in SSB/R usually was greater than the progressive loss in Y/R for refuges of increasing size (Fig. 2).

Another general pattern was the relative importance of the interactive effect of natural and fishing mortality rates, compared to age at recruitment to the fishery. For most combinations of M and F_c, B/R was more strongly influenced by these two rates than by age at recruitment (Fig. 4, Table 3). Depending on fish type, B/R values ranged two- to five-fold as M and F_c values varied ±50% of their midpoint estimates, but ranged only twofold or less as A_c varied ±50% (Table 3).

By comparison, transfer rates had relatively little effect on SSB/R, compared with the effects of natural and fishing mortality rates. For a median-sized closure of 25%, changes in percentage of virgin SSB/R differed <10% within fish type for transfer rates that varied as much as two orders of magnitude (Fig. 3).

Another generality, not previously made explicit, is that ages at maturity and at first capture can more strongly influence spawning stock than can the presence and size of a refuge. The presence of a refuge will have a relatively weak effect on spawning biomass if the resource begins to be heavily exploited well before sexual maturity. In extreme cases, SSB/R might not be appreciably enhanced by large closures, despite relatively low transfer rates.

Fish types

Perhaps the most significant, specific result of the simulations was that fish types differed in how refuge size affected SSB/R levels. Large, apparent gains in percent virgin SSB/R of the damselfish occurred only at the expense of large losses in yield (Figs. 1A, 2A, 3A). Nontrivial (>5%) gains in percentage SSB/R of surgeonfish could occur at small (0.1) refuge sizes, although the overall rate of increase in SSB/R would be greater for larger closures (Figs. 1B, 3B). For the jack, however, gains in SSB/R of magnitude similar to those of the surgeonfish could be realized with increasing refuge size only for large ($R_1 > 0.3$) closures (Figs. 1C, 3C).

Simulation results appeared to vary among fish types in response to their differing growth rates and natural mortality and exploitation schedules. For example, in comparing the results for the high-mortality surgeonfish with those for the low-mortality jack, substantive gains in SSB/R of the jack (restricted to large closures) were further restricted to low ($F_c \leq 0.4$) levels of fishing effort (Fig. 1C). SSB/R dropped below 20% of the virgin stock at $F_c = 0.3$, the fishing effort that was optimal for maximizing Y/R (Fig. 1C). For the surgeonfish, appreciable (≥10%) gains in SSB/R could occur under heavy ($F_c > 1$) exploitation rates for refuges as small as 10–20% (Fig. 3B), and ≥20% of virgin SSB/R can be sustained at $F_c \leq 1.15$ (Fig. 1B).

The observed differences among fish types in the potential for MFRs to increase SSB/R also were strongly influenced by the ages at sexual maturity and recruitment to the fishery. Ages at first maturity and at first capture were attributes that differed greatly among the three fish types (damselfish: age 1; surgeonfish: age 2; jack: age 4; Table 2). Median B/R (equal to SSB/R for all except the damselfish at A_c = 0.5 year) varied by 30% for the damselfish, 100% for surgeonfish, and 35% for the jack among ages at first capture that varied ±50% of their respective midpoints (Table 3). Compared with age at first catch, transfer rates had less effect; SSB/R consistently varied ≤10% for the damselfish (with twofold variation in very low transfer rates; Fig. 3A), for the surgeonfish (with fivefold variation in moderate transfer rates; Fig. 3B), and for the jack (with tenfold variation in rapid transfer rates; Fig. 3C). At a reference F_c of 1.0 and a median closure size of 25%, SSB/R varied from <6 to 35% of virgin stock biomass, depending on fish type (Fig. 1, A–C).

Compensatory transfer rates

Even small (eighth root of density ratio) compensatory increases in transfer rates could have negated potential increases in SSB/R that might result from the presence of a closure. A larger adjustment with the square root of the density ratio, of course, can have an

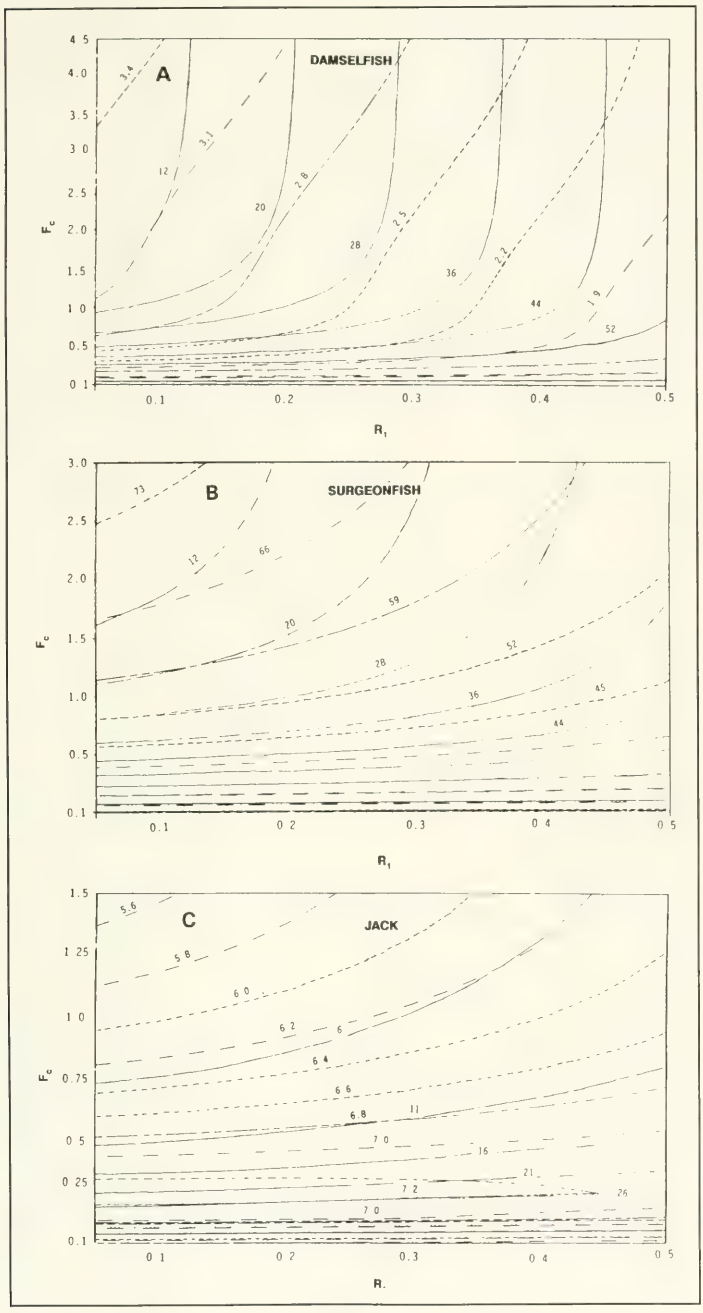

Figure 1

Overlay of a yield-per-recruit surface (various dashed lines) on a percentage spawning stock biomass-per-recruit surface (solid lines) as a function of refuge size (R_j) and fishing mortality rate (F_c) when transfer rate (T_{1c}) is constant: (**A**) damselfish (T_{1c} = 0.01); (**B**) surgeonfish (T_{1c} = 0.25); and (**C**) the jack (T_{1c} = 0.5). Spawning biomass values are expressed as a percentage of virgin biomass that would accrue if no fishing were allowed in areas 1 and 2.

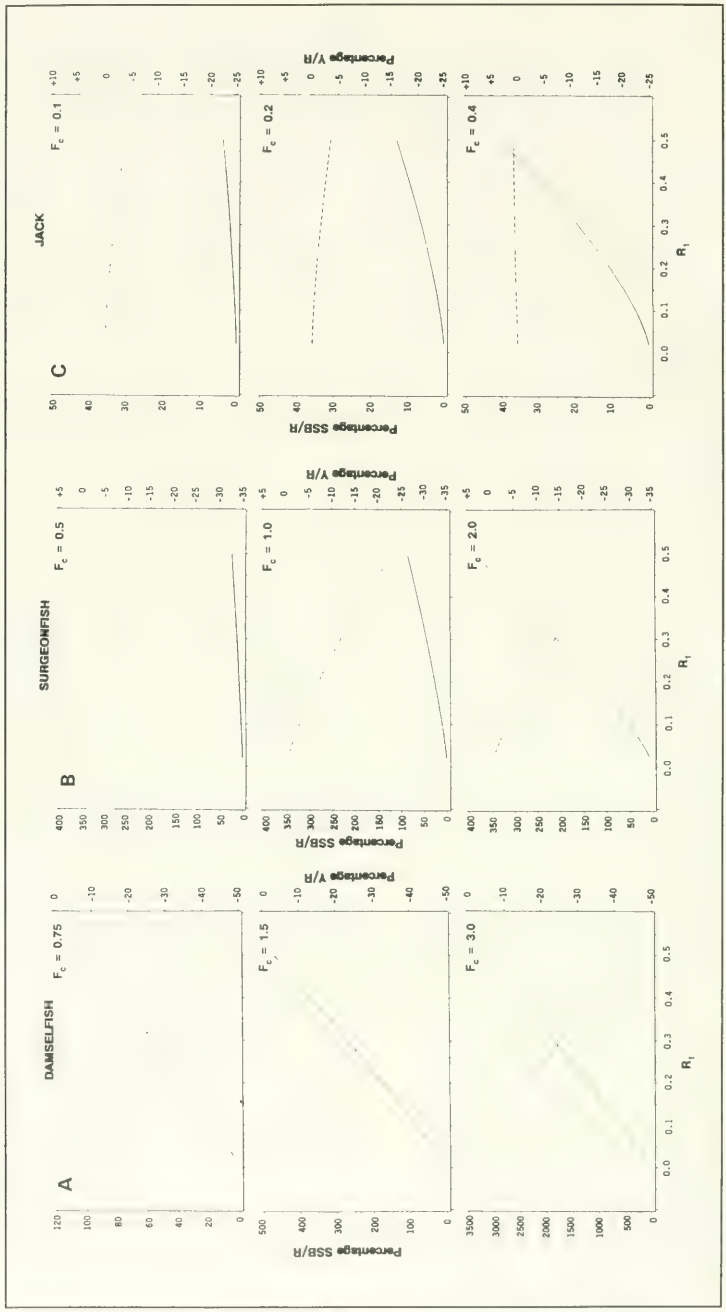

Figure 2

Percentage changes in spawning stock biomass per recruit (SSB/R; solid line) and yield per recruit (Y/R; dashed line) as a function of refuge size (R_1), when transfer rate (T_1) is constant, for different fishing mortality rates (F_c): (**A**) damselfish (T_1 = 0.01); (**B**) surgeonfish (T_1 = 0.25); and (**C**) the jack (T_1 = 0.5). Spawning biomass and yield values are standardized by the biomass and yield that would accrue if there were no closure (i.e., both areas 1 and 2 open).

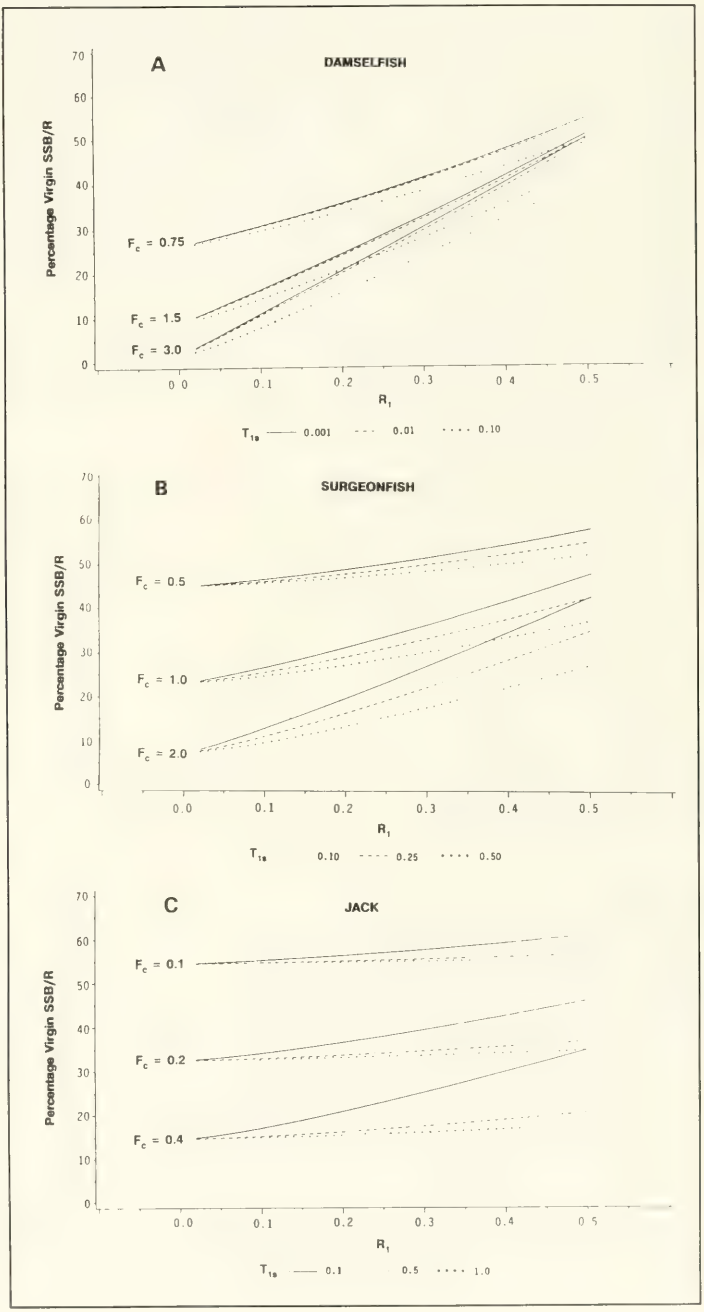

Figure 3

Relative changes in spawning stock biomass per recruit (SSB/R) as a function of refuge size (R_1) compared at fishing mortality rates (F_c) equal to natural mortality rates (M) of $0.5M$, M, and $2M$, among a range of possible fundamental transfer rates (T_{1a}) for (**A**) damselfish (in grams), (**B**) surgeonfish (in grams), and (**C**) the jack (in kilograms). SSB/R values are standardized by the respective virgin biomass value that would accrue if no fishing were allowed in areas 1 and 2.

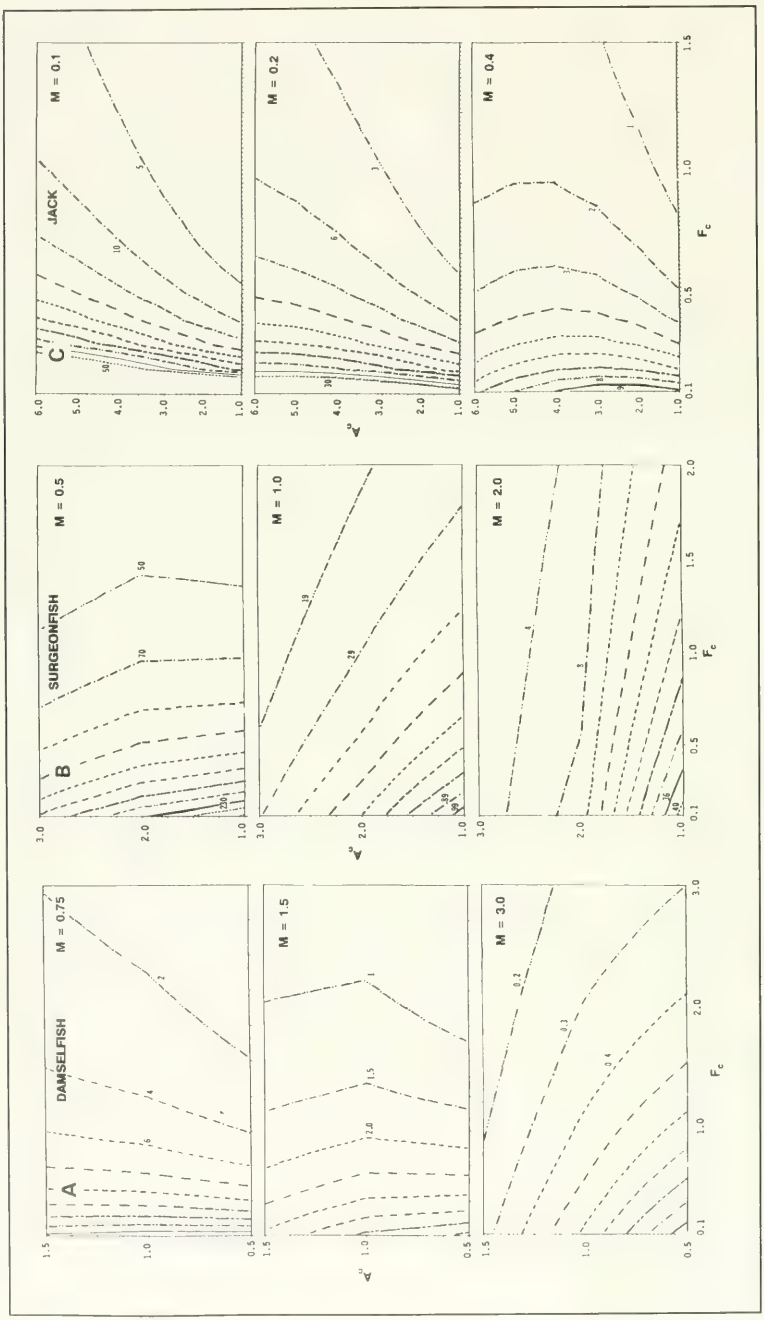

Figure 4

Stock biomass per recruit (B/R) surfaces as a function of fishing mortality rates (F_c) and age-at-recruitment to the fishery (A_c) for (**A**) damselfish (in grams), (**B**) surgeonfish (in grams), and (**C**) the jack (in kilograms).

Table 3

Equilibrium B/R (total biomass per recruit) values without any refuge at select combinations of A_c (age-at-first-capture), M (natural mortality rate), and F_c (fishing mortality rate) for each of the three fish types. See text Methods, Table 1, and footnotes to Table 2 for basis of chosen A_c and M values. F_c was evaluated at values equal to $0.5M$, M, and $1.5M$. B/R at the most reasonable (midpoint) values of A_c and M are emphasized in bold and underlined type, respectively, and the relative influences of A_c, M, and F_c on B/R are noted. A_c = 0.5 year (damselfish) and 1.0 year (surgeonfish and jack).

Damselfish B/R (g)

	A_c = 0.5			A_c = **1.0**			A_c = 1.5		
At M =	0.75	1.5	2.25	0.75	1.5	2.25	0.75	1.5	2.25
If F_c = 0.75	5.4	2.1	1.1	**6.7**	**2.3**	**1.0**	7.4	1.9	0.6
1.50	2.1	1.1	0.7	**3.3**	**1.4**	**0.7**	4.0	1.2	0.4
2.25	1.1	0.7	0.5	**2.0**	**1.0**	**0.5**	2.6	0.9	0.3

$M = F_c >> A_c$

Surgeonfish B/R (g)

	A_c = 1.0			A_c = **2.0**			A_c = 3.0		
At M =	0.5	1.0	1.5	0.5	1.0	1.5	0.5	1.0	1.5
If F_c = 0.50	119.9	66.8	44.8	**110.0**	**40.5**	**17.4**	85.4	19.9	5.3
1.00	66.8	44.8	33.2	**66.7**	**28.7**	**13.4**	54.0	14.4	4.2
1.50	44.8	33.2	26.2	**47.3**	**22.1**	**10.9**	39.2	11.3	3.4

$M > F_c = A_c$

Jack B/R (kg)

	A_c = 2.0			A_c = **4.0**			A_c = 6.0		
At M =	0.1	0.2	0.3	0.1	0.2	0.3	0.1	0.2	0.3
If F_c = 0.1	96.4	36.6	17.6	**112.3**	**40.3**	**18.0**	123.0	39.8	15.6
0.2	40.4	19.4	10.8	**54.5**	**24.3**	**12.2**	65.6	25.8	11.3
0.3	21.5	11.9	7.3	**32.8**	**16.5**	**9.0**	42.5	18.6	8.7

$M > F > A$

even larger countering effect (Fig. 5). The effect of compensatory rate adjustments apparently varied with fish type in a manner not directly related to fundamental transfer rate. When the surgeonfish and jack were each evaluated using $T_{1/2}$ = 0.1 as the fundamental rate, compensatory dampening in the rate of SSB/R gain at larger refuge sizes was less for the surgeonfish (Fig. 5A) than for the jack (Fig. 5B).

Discussion

MFRs and enhanced Y/R

Simulations to date suggest that MFRs have the potential to augment SSB/R, but enhance Y/R little, if at all, in adjacent non-closed areas (Polacheck, 1990; the present study). The only empirical study to date was inconclusive: Alcala and Russ's (1990) observations of an effect on reef fish catches adjacent to the Sumilon Island reserve were from a series of years in which the reserve operated and from only one year of reduced catches that began 18 months after the reserve's protected status ended. Catches were dominated by one taxon (fusiliers, family Caesionidae; 65% of total) that used the reef for nocturnal shelter but whose zooplankton prey may have been unrelated to reef area (Alcala and Russ, 1990). Brief changes in yield, rather than Y/R, particularly on a small (0.5 km^2) spatial scale, may represent nonequilibrium phenomena (e.g., lagged effects on adult abundance resulting from a localized change in recruitment). Alcala and Russ's (1990) observations therefore are not necessarily inconsistent with simulation results (see Russ et al., in press).

Clearly, additional empirical measures are needed for Y/R as well as SSB/R of fishery resources in exploited regions adjacent to MFRs. For the present discussion, however, this paper will focus on simulated SSB/R results.

Relative influences of input parameters

Growth rate is a major influence of biomass accrual within refuges (Polacheck, 1990), as fast-growing fish can elaborate more surplus production (yield) per unit time and unit area of refuge than can slow-growing fish. And since growth and mortality rates are linked, it is not surprising that mortality rate is important, as fishes with a higher natural mortality can support fisheries in which they are harvested more heavily and earlier in life than can fishes with a lower mortality rate.

In the basic yield model, the effects of natural mortality and level of exploitation overwhelm those of age at first capture. Proportional changes in rates obviously have larger effects than equal-sized changes in the time period over which the rates apply. Of greater interest here are the relative magnitudes of the effects

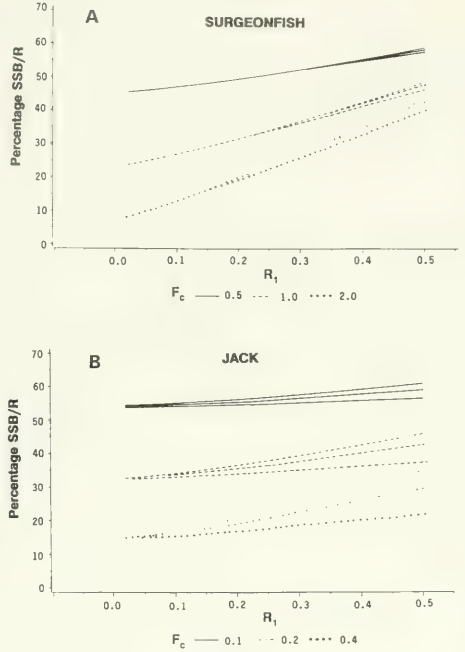

Figure 5

Percentage changes in spawning stock biomass per recruit (SSB/R) as a function of refuge size (R_1), fundamental transfer rate (T_{1c}), and two levels of density-dependent, compensatory adjustment of this fundamental rate: (**A**) surgeonfish (T_{1c} = 0.1); (**B**) jack (T_{1c} = 0.1). Within each triplet of lines, the upper, middle, and lower line depicts the unadjusted, adjusted 0.125-power, and adjusted 0.5-power rate, respectively.

of ages at sexual maturity and first capture, versus those of refuge size and transfer rates. I suggest that the former can have large influences for relatively short-lived, fast-growing species like the surgeonfish for which changes in age at first capture of only ±1 year represent a large fraction of its life span.

Circumstantial evidence suggests that the relative ages at sexual maturity and first capture can be important. Prior evaluations of the potential for MFRs to conserve the *SSB* of overfished commercial stocks (e.g., red snapper, *Lutjanus campechanus*) have concurrently considered other management safeguards, such as size limits in the non-closed area (Plan Development Team, 1990). However, nearshore reef fishes subject to recreational harvest are often fished at sizes and ages considerably less than those at sexual maturity, even on moderately populated islands (e.g., the island of Hawaii; Hayes et al., 1982). For reef fishes near densely populated areas where exploitation is likely to be intense on pre-reproductive fish, the potential for MFRs to enhance SSB/R may be severely compromised, even at closure sizes that are as large as is practical (e.g., 25%).

Compensatory emigration

Density-dependent increases in the fundamental transfer rate can in essence depress potential gains in SSB/R in a manner analogous to that of a higher but constant fundamental transfer rate. The observation that gains in SSB/R at increasingly large refuge sizes were strongly offset by compensatory movements in the jack, but not in the surgeonfish, perhaps reflects the jack's slower growth rate, greater longevity, and lower mortality rate. Longevity, per se, may be important, because the model that was used to describe compensatory emigration is dependent upon time as well as age.

SLOSS effects on MFR function

Simberloff (1988) reviewed the SLOSS concept and the meager results to date regarding whether multiple, small reserves function the same as single reserves of equal total size. Historically the issue of SLOSS has been applied to the preservation of threatened and endangered species or the conservation of biotic diversity (Bell and Boecklen, 1990, but see Goeden, 1979). It is increasingly apparent that meaningful stewardship of the environment and its biota extends beyond these simple (although often difficult to implement) criteria. Overexploiting an ecosystem's productivity by overfishing (Russ, 1991) is just as detrimental as recruitment or growth overfishing.

Bohnsack (1991) recently applied the SLOSS concept in a review of the function of artificial reefs. Obviously MFRs also can be evaluated in terms of SLOSS—the question then may be, "Do several small reserves potentially enhance SSB/R to the same extent as one reserve of equivalent total size?" A realistic example may be the relative fishery enhancement potential of ten 1% closures versus one 10% closure. Establishing a MFR of 10% may be impossible on a heavily populated island (like Oahu, Hawaii) where shoreline development is near saturation. The siting of multiple, smaller refuges, each about 1% of the total area, may be feasible, however. But can a total closure of realistic size (10%) be beneficial, and can the potential of ten 1% closures approximate it?

The simulation results suggest that a total closure of 10% may enhance the spawning stock of a fast-

growing, moderately vagile reef species such as surgeonfish: at a fishing mortality rate (F_c) of 1.0 (equal to M = 1.0), SSB/R can be increased by about 24% over the no-closure case for an MFR of 10%, if the lower bound of T_{1s} (0.10) is used as the fundamental emigration rate. By using the higher bound for T_{1s} (0.5) and an F_c still at 1.0, SSB/R is increased by 12% for the single 10% closure.

The overall contribution of multiple, small closures will be less, however, than that of one closure of equal total size, in inverse proportion to the increase in the total perimeter of (hence dispersal from) the multiple closures. (This follows from the general rule that smaller reserves have greater perimeter-to-area ratios than larger reserves of equivalent shape [Schonewald-Cox and Bayless, 1986].) In our example, the total perimeter of ten 1% closures is about three times ($\sqrt{10}$) that of one 10% closure. Hence, for a given fundamental transfer rate, the actual transfer rate will be appreciably greater, and the additive contribution of ten 1% closures to SSB/R will be several times less, than that of one 10% closure. Multiple 1% closures might translate to an actual emigration rate approaching 0.5 for a surgeonfish that is moderately vagile (T_{1s} = 0.1–0.25) relative to an MFR of 10%.

For the preceding arguments to hold, we must further assume that the multiple closures will not interact spatially. It seems reasonable though that for post-settlement stages of species with low fundamental transfer rates, ten 1% reserves may function independently if well-spaced, perhaps even on a relatively small (e.g., 100-km perimeter) island such as Oahu, Hawaii.

For simplicity, SLOSS arguments generally ignore the interactive effects of refuge shape and size. However, habitat geometry (shape as well as size) importantly influences dispersal into and from a habitat, regardless of whether an organism's movements are home-ranging or free-ranging (Stamps et al., 1987). Edge "permeability" (i.e., whether a reserve is sited within a larger area of homogeneous "soft-edged" habitat or is a functional island surrounded by discontinuous "hard-edged" habitat) also significantly affects dispersal (Buechner, 1987; Stamps et al., 1987). Small increases in edge permeability have disproportionately large effects on dispersal when boundaries are hard, whereas habitat shape exerts a controlling influence on dispersal when boundaries are soft (Buechner, 1987; Stamps et al., 1987). For shoreline-bounded reef closures, the shape of the MFR is clearly more important to residential reef fishes if the MFR is sited within a larger region of similar habitat than if different habitats (e.g., extensive sand channels) are used to provide its physical boundaries.

Future research

The overall net effect of the diverse compensatory and depensatory factors that may influence the movement patterns of fishes into and out of MFRs is beyond even semiquantitative appraisal at present. Major advances in our understanding of the function of MFRs await development of techniques that describe the fundamental transfer rates of fishes (Polacheck, 1990) and that further estimate the changes in movement rates that may occur as densities change over time. The results of my preliminary analyses suggest that future studies should focus on fast-growing, moderately vagile species such as many surgeonfishes, rather than reef transients or philopatriots. My preliminary conclusions should be reevaluated as more data become available for these and other types of reef fishes.

Management potential

MFRs have the potential to enhance the biomass and spawning stock of species with rapid growth and moderate, fundamental transfer rates (Polacheck, 1990; the present paper). Many factors, however, contribute to whether this potential is likely to be realized in practice: the age schedule of harvest and the magnitude of fishing effort in the non-closed area; whether one versus a few or many MFRs of a given total area are used, thereby promoting progressively larger increases in fundamental transfer rates; and whether compensatory emigration acts to further inflate vulnerability and deflate SSB/R. Decisions as to the number versus size of MFRs that can be sited, given the total shoreline extent of reef available, are social issues. Size limits and fishing effort (bag limits) also are subject to their own management politics, and MFRs will not make them obsolete. Although the fast growth and moderate movement rates of certain tropical reef fishes predispose them to benefit from refuges, it is unlikely that the establishment of MFRs alone, without complementary regulation of effort and the size composition of catch in non-closed areas, can augment the SSB/R of fishes on heavily exploited island reefs.

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Allometry of energetics parameters in spotted Dolphin *(Stenella attenuata)* from the eastern tropical Pacific Ocean

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Abstract.—Interest in estimating energy fluxes through populations of marine mammals has been increasing as these populations are more frequently recognized to compete with fishermen for commercially exploited fish stocks. Testing for the presence of allometric trends with size in the parameters used to estimate these energy fluxes is important because if such trends exist and are large, it will be inappropriate to apply measurements derived from one size of animal to animals of other sizes, in any given population. To test for (and to measure, if present) allometric effects in a population of small cetaceans, morphological measurements (energetics parameters) related to estimating energy flux were taken from 35 spotted dolphins (*Stenella attenuata*) ranging in size from 77 to 210 cm total length, captured incidental to fishing operations in the eastern tropical Pacific Ocean.

Significant allometric (nonlinear) changes with size were observed in 23 of the 25 parameters measured; no trends were isometric (linear). Most of the significant trends were expressed primarily during the first two or three years of life (5–30 kg wet weight). Thus, parameter estimates for small dolphins (less than about 30 kg wet weight) should be derived from measurements on animals near the specific size of interest. Estimates for larger animals, with the exception of several surface area measurements, could be estimated reasonably well from any specimens greater than about 30 kg wet.

Although the energy fluxes and standing stock of energy represented by animals younger than 2–3 years are relatively small compared with the total population, constraints resulting from the energy characteristics of the smaller animals may exert significant control over population energy flux, implying that the rapid changes in energetics parameters of the younger animals should not be ignored.

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Estimating cetacean population energy fluxes, in particular energy consumption in the form of commercially valuable fishes, is important because many commercially exploited fish populations are decreasing in abundance yet must be shared by both human and cetacean predators. The existence in cetacean populations of allometric trends (nonlinear changes with size) in morphological characteristics related to energy processing complicates energy flux estimation for these animals because the size range of cetacean specimens available for study tends to be very narrow. If allometric trends are present and large, measurements from that narrow size range cannot be assumed to apply equally to all other sizes in the population.

Neither commercial nor noncommercial sources of cetacean specimens generally provide an adequate range of sizes from which to determine whether allometric trends exist. Specimens available from commercial sources will include only those sizes sought by the fishery. For example, morphological samples from large cetaceans (whales) tend to be dominated by adult (and when pregnant females are captured, by fetal) specimens because the larger individuals have more commercial value. Juveniles are rarely captured. Morphological samples from small cetaceans (dolphins and porpoises) are rare for all sizes because these animals are rarely the subject of directed fisheries. Specimens from noncommercial sources are generally available only as beached or stranded individuals, or where observer programs are employed to monitor kill rates of both target and nontarget species. These noncommercial specimens tend to be too rare to provide an adequate sample of sizes.

In addition to these sampling biases in age and species composition, the data collected are generally unsuitable for deriving estimates of energy flux. Although considerable morphological data exist for commercially exploited large whales (e.g., Fujino 1954, 1956; Omura and Fujino, 1954; Omura and Sakiura, 1956; Ohsumi, 1960; Nishiwaki et al., 1963; Lockyer, 1981, a and b, and references therein) and a few similar reports exist for small cetaceans (e.g., Sergeant, 1962;, Perrin, 1975; Yasui, 1980; Perrin et al., 1987), these data generally include only a standardized set of external morphological measurements used primarily for taxonomic purposes. Taxonomic data tend to be inappropriate for deriving estimates of energy flux because many size classes and most of the morphological measurements required specifically for energetics estimates are missing.

Although some estimates have been developed for energy processing in neonate through adult large whales (Lockyer, 1981, a and b), allometric trends in energetics parameters have never been examined in

small cetaceans. Existing studies of small cetaceans include only Yasui and Gaskin's (1986) energy budget for adult harbor porpoise (*Phocoena*), in addition to a few estimates for various aspects of energy processing by juvenile (e.g., Anderson, 1981) or adult (e.g., Lang, 1966; Lockyer, 1981, a and b; Yasui and Gaskin, 1986; Hui, 1987; Bose and Lien, 1989; Bose et al., 1990) small cetaceans.

Incidental mortality of spotted dolphins (*Stenella attenuata*), a small cetacean that is inadvertently killed during some tuna purse-seining operations in the eastern tropical Pacific Ocean (ETP), presents an exception to this problem of specimen unavailability. Specimens of all sizes die in purse-seines (Barlow and Hohn, 1984; Hohn and Hammond, 1985), making it possible to collect appropriate data for the entire size range occurring in the natural population.

Taking advantage of this availability of specimens, spotted dolphins ranging in size from fetal through mature adult were collected from the fishery and analyzed for morphological characteristics related to energy processing. I report here regression equations relating changes in 25 energetics parameters to changes in total wet weight for these specimens. The parameters can be used in estimation of three components contributing to cetacean energy budgets: active metabolism, passive heat loss, and energy density. Estimated energy density is derived from a subset of the measured parameters and is reported as the 25th parameter. Total energy budgets, active metabolism, and passive heat loss are not estimated here because such estimates depend on various assumptions about other factors (e.g., environmental conditions, activity levels) and other energy budget components (e.g., standard metabolism, heat of digestion) not included in this study. The work reported here was conducted to determine the extent to which allometric trends, if any, could be determined from simple morphological measurements on deceased cetaceans.

Methods and materials

Specimen collection

Measurements were taken from 35 spotted dolphins ranging in size from 71 to 210 cm total length (TL [tip of rostrum to fluke notch] Fig. 1). This represents the entire size range (near-term fetus through mature adult) of the spotted dolphins found in the eastern tropical Pacific Ocean (spotted dolphins are about 80 cm total length at birth (Hohn and Hammond, 1985)). Specimens included 22 females and 13 males (Table 1). Males specimens included 3 fetuses, 6 immature, and 4 mature. Females specimens included 3 fetuses, 6 immature, 1 mature resting, 1 mature lactating, and 11 mature pregnant. Not all measurements were made on all specimens. All specimens were collected incidental to tuna fishing operations in the eastern tropical Pacific Ocean. Seventeen of the specimens were collected on 28 December 1985; nine were collected during July and two during August 1985 (Table 1). Specimens were kept frozen after collection and were thawed in fresh water (about 27°C) just prior to sampling for energetics parameters.

Parameter measurements

Active metabolism Active metabolism in cetaceans is the total energy cost of swimming, i.e., energy (mechanical plus waste heat production heat) expended to overcome hydrodynamic drag. Cost of steady submerged swimming by cetaceans can be estimated by using Magnuson's (1978) procedure for estimating cost of swimming by tuna (see also Webb, 1975), including drag on both body and fins. Eleven morphological measurements are required to estimate hydrodynamic drag: maximum diameter of the body (D_{max}); wetted surface areas of the body (WSA_b), flippers (WSA_{fp}), dorsal fin (WSA_d), and flukes (WSA_{fl}); mid-chord depths of flippers (MCD_{fp}), dorsal fin (MCD_d), and flukes (MCD_{fl}); and characteristic length of flippers (CL_{fp}), dorsal fin (CL_d), and flukes (CL_{fl}) (Table 2).

D_{max} was derived from measurements of body circumference immediately anterior to the dorsal fin (C_3;

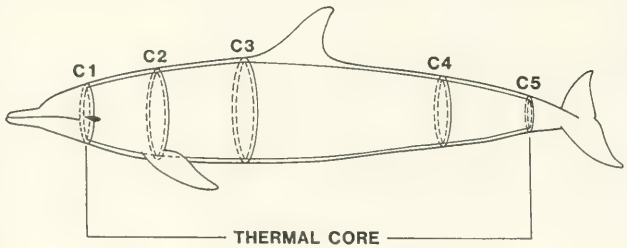

Figure 1
Locations of the 5 **circumference measurements** on dolphin specimens. Thermal core (metabolic surface area) extends from eye to mid-caudal peduncle (*sensu*, Brodie, 1975). C1: at eye, C2: at axilla, C3: just anterior to dorsal, C4: at anus, C5: at mid-caudal peduncle.

Table 1
Collection data for dolphin specimens.

Specimen no.	Spec. Code	wet weight (gm)	total length (cm)	Sex	Reprod.[1] condition	Date captured	Location (lat.)	Captured (long.)	D_{max} (cm)	BD_d (cm)
1	BXR252	27013	132	F	I	12/28/85	17°46'N	111°37'W	71.8	0.75
2	BXR253	68100	194	F	M-R	12/28/85	17°46'N	111°37'W	95.0	0.97
3	BXR254	73775	192	F	M-P	12/28/85	17°46'N	111°37'W	103.2	0.86
4	BXR254F	4983	78	M	F	12/28/85	17°46'N	111°37'W	35.4	0.45
5	BXR255	64540	186	F	M-P	12/28/85	17°46'N	111°37'W	107.5	1.08
6	BXR255F	5800	78	F	F	12/28/85	17°46'N	111°37'W	40.8	0.68
7	BXR264	62425	183	F	M-P	12/28/85	18°09'W	111°17'W	97.8	0.82
8	BXR264F	3760	71	F	F	12/28/85	18°09'W	111°17'W	34.0	0.51
9	BXR271	24516	136	M	I	12/28/85	18°09'W	111°17'W	66.9	0.83
10	BXR280	19976	127	M	I	12/28/85	18°09'W	111°17'W	61.0	0.68
11	BXR282	76272	193	F	M-P	12/28/85	18°09'W	111°17'W	103.0	1.00
12	BXR295F	4200	74	F	F	12/28/85	18°09'W	111°17'W	34.6	0.52
13	BXR306	37228	163	F	I	12/28/85	18°09'W	111°17'W	75.0	0.90
14	BXR312	35639	152	F	I	12/28/85	18°09'W	111°17'W	75.0	0.88
15	BXR313	63787	175	F	M-P	12/28/85	18°09'W	111°17'W	97.6	0.92
16	BXR(A284F	3410	71	M	F	12/28/85	18°09'W	111°17'W	34.8	0.45
17	BXR(A)284	69689	191	F	M-P	12/28/85	18°09'W	111°17'W	100.4	NR
18	SRMO44(F)	5400	81	M	F	2/14/80	06°02'S	85°46'W	40.0	0.73
19	WFP660	16400	114	F	I	NR	NR	NR	55.0	NR
20	WFP680	30900	136	M	I	7/7/83	NR	NR	74.0	NR
21	SRMO44	73100	189	F	M-P	2/14/80	06°02'S	85°46'W	110.0	0.97
22	WFP700	48124	170	M	M	NR	NR	NR	84.6	0.61
23	PEL307	42903	167	F	I	7/10/85	8°55'N	129°58'W	80.0	0.70
24	PEL308	41314	151	M	I	7/10/85	8°55'N	129°58'W	81.0	0.72
25	PEL309	74002	189	F	M-P	7/13/85	8°13'N	129°40'W	99.0	0.95
26	PEL310	71732	202	F	M-P	7/13/85	8°13'N	129°40'W	97.5	0.85
27	PEL311	55388	176	F	M-P	7/14/85	10°21'N	129°35'W	91.0	NR
28	PEL313	72640	202	M	M	7/14/85	10°21'N	129°35'W	94.2	0.66
29	PEL314	44265	160	M	I	7/14/85	10°21'N	129°35'W	85.4	0.69
30	PEL315	69008	188	M	M	7/14/85	10°21'N	129°35'W	95.5	0.82
31	PEL316	58566	175	F	M-P	7/14/85	10°21'N	129°35'W	94.0	0.87
32	SD1	11350	100	M	I	NR	NR	NR	53.5	0.71
33	SD2	14301	113	F	I	NR	NR	NR	56.0	0.61
34	STB122	84444	206	M	M	8/30/85	10°14'N	125°03'W	98.0	0.86
35	STB126	74202	188	F	M-L	8/30/85	10°14'N	125°03'W	102.0	0.64

[1]F = fetus; I = immature; M = mature; M-R = mature resting; M-P = mature pregnant; M-L = mature lactating; NR = no record.

Fig. 1). WSA_b was measured as the sum of surface areas of right circular cones. Conic surfaces were calculated from measurements of body circumference at five locations and distances from tip of rostrum to each circumference and to fluke notch (Fig. 1).

WSA_{fp}, WSA_d and WSA_{fl} were estimated by tracing the perimeter of each fin onto white paper, measuring with a digitizer the surface enclosed, correcting for curvature, and multiplying by 2. Both flukes were traced as a unit. Each dorsal fin and flipper was traced separately.

The correction for curvature along fin surfaces was derived from one small (132 cm TL) and one large (193 cm TL) dolphin. Flippers, flukes, and dorsal fin from each specimen were sliced laterally into 4 or 5 sections. The cross-section of each piece was then xeroxed onto white paper. Distances straight across and around the perimeter of each cross-section were then measured twice for each cross-sectioned piece of fin. There were no significant differences between fins or sizes of dolphin in the ratio of curved to flat measurements so a single correction was used for all fins. The curvature correction was an increase of 6% over the estimated flat area of each fin (3% per side; SE = 0.4; n = 23 sections).

MCD_{fp}, MCD_d, and MCD_{fl} were measured to the nearest millimeter by using calipers at the thickest part of each fin at the mid-point of the characteristic length.

Table 2
Symbols and definitions.

ACT	active metabolism (calories active metabolism calorie animal $^{-1}$·hr $^{-1}$)
BD_a	average blubber depth (cm)
C_f	coefficient of friction drag
C_T	coefficient of total drag
CD_d	caloric density of dolphin (cal g wet weight $^{-1}$)
CL_{fp}	characteristic length of the flippers (cm)
CL_d	characteristic length of the dorsal fin (cm)
CL_{fl}	characteristic length of the flukes (cm)
D_{max}	maximum diameter of the body (cm)
D_T	total drag (dyn)
ED_{an}	energy density of total animal (mJ/kg wet weight)
ED_{bl}	energy density of blubber (mJ/kg wet weight)
ED_m	energy density of muscle (mJ/kg wet weight)
ED_b	energy density of bone (mJ/kg wet weight)
F_m	fraction of body wet mass due to muscle
F_b	fraction of body wet mass due to blubber
F_b	fraction of body wet mass due to bone
F_v	fraction of body wet mass due to viscera
F_f	fraction of body wet mass due to fins
FID	fin-induced drag (fraction of total drag)
H_u	minimum unavoidable heat loss (calories lost as heat calorie animal^{-1}·day^{-1})
MCD_{fp}	mid-chord depth of the flippers (cm)
MCD_b	mid-chord depth of the dorsal fin (cm)
MCD_{fl}	mid-chord depth of the flukes (cm)
ME	mechanical efficiency
MP	mechanical power (erg/s)
MSA_b	metabolic surface area of the body (cm^2)
N	density of sea water (g/cm^3)
PE	propeller efficiency
R_l	Reynolds number based on length L (dyn/cm^2)
TL	total length (cm)
υ	kinematic viscosity (stoke)
VL	velocity (cm.sec^{-1})
WSA_b	wetted surface area of the body (cm^2)
WSA_{fp}	wetted surface area of the flippers (cm^2)
WSA_f	wetted surface area of the dorsal fin (cm^2)
WSA_{fl}	wetted surface area of the flukes (cm^2)
WW_a	total body wet weight (g)
$\%H_2O_{bl}$	water content of blubber (percent of wet weight)
$\%H_2O_m$	water contents of muscle (percent of wet weight)
$\%H_2O_b$	water contents of bone (percent of wet weight)

CL_{fp}, CL_d, and CL_{fl} were estimated from the traced figures, by measuring the length of the fin parallel to the main axis of the body.

Unavoidable passive heat loss (HL_u) Unavoidable passive heat loss was defined as heat loss due to conduction through blubber, if one assumes no heat loss from appendages or from the head anterior to the eyes (e.g., Brodie, 1975). Two morphological measurements contribute to this estimate of HL_u; metabolic surface area of the body (MSA_b) and average blubber depth (BD_a). MSA_b was estimated by the same method as wetted surface area, except that the first anterior and last posterior sections of the body (Fig. 1) were omitted from the assumed thermal core and the conic radius used in the estimate was the radius of the body core beneath the blubber. This metabolic radius was estimated by determining the radius to the outer surface at each circumference and by subtracting the average blubber depth measured at that circumference. Two or three measurements of blubber depth were made along each circumference at the dorsal midline, ventral midline, and mid-way between these two lines.

BD_a for the entire animal was estimated as the weighted sum of average blubber depths at each circumference. Weightings were the circumferences themselves, which gives more weight to the relatively symmetrical mid-body areas that comprise the majority of the insulating area, and less weight to the thick average blubber depths related to the hydrodynamic keel in the tail region.

Energy density Eleven morphological measurements contribute to estimating the overall energy density of an individual spotted dolphin (ED_{an}): fractions of wet mass due to muscle (F_m), blubber (F_{bl}), bone (F_b), viscera (F_v), and fins (F_f); energy densities of blubber (ED_{bl}), muscle (ED_m), and bone (ED_{bn}); and water contents of blubber ($\%H_2O_{bl}$), muscle ($\%H_2O_m$), and bone ($\%H_2O_{bn}$). Energy content of body fluids (blood, interstitial fluids) were ignored. Fluid losses accounted for about 10% of the difference between total weights of undissected specimens and the sum of dissected body fractions.

F_m, F_{bl}, F_{bn}, F_v and F_f were determined by measuring the total wet weight of each specimen, and by dissecting the specimen into component parts and weighing each component. Skeletal weight was determined after carefully flensing and scraping all tissue from each bone, including tissue between ribs, between spinal column processes, and within the skull and jaw structures. ED_{bl}, ED_m, and ED_{bn} were determined by bomb calorimetry (Cummins and Wuycheck, 1971). Data used in regressions are means of two or four replicate energy density determinations. Dry weights were determined after freeze-drying samples to constant weight (48 hours) and storing in a desiccator for 24 hours. Ash-free dry weights were determined after ashing samples at 450°C for 4 hours and cooling for 24 hours in a desiccator. Dry and ash-free dry weight determinations were made on samples of 1–20 g wet weight. $\%H_2O_{bl}$, $\%H_2O_m$ and $\%H_2O_{bn}$ were calculated as

$$(1.0 - (\text{dry weight/wet weight})) * 100.$$

Energy density (ED_{an}) of entire dolphins was estimated as the weighted sum of predicted energy densi-

ties of blubber, muscle, viscera, bone, and fins, where weightings were the predicted fractions of total wet body mass for each tissue type. Energy density of viscera was assumed to be the same as energy density of muscle, based on the relatively muscular nature of these organs (compared with bone or blubber) and the absence of any visible fat deposits upon or within organs. Errors were assumed negligible because the viscera comprised a relatively small fraction of total body weight and it appeared unlikely that the viscera represented a major lipid depot in these tropical cetaceans. Energy density of fins was assumed to be the same as energy density of bone, based on the assumption that caloric content of cartilage (the actual composition of fin material) is closer to bone than to either muscle or blubber. Again, errors due to this assumption should be relatively small as the fins contribute very little to overall body weight. Estimated total energy density is presented as a function of the regression-predicted values of each parameter, where parameter variances are ignored.

Data analysis

Relationships between morphological measurements and total wet weight were determined by using linear regression analysis of log transformed variables, where morphological measurements and wet weights were converted to logarithms (base 10) prior to analysis.

Results

Significant allometric trends ($P < 0.05$) occurred in 23 of the 25 parameters (Table 3; Figs. 2–11). No signifi-

Table 3

Regression equation parameters relating energetics parameters to total wet weight of spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean. Regressions performed on log10-transformed data in both X and Y. Re-transformed equation of the form $Y = aX^b$. X units are wet weight in kg. Y units are as noted. Symbols are defined in Table 2.

			n[1]	b[2]	se(b)[3]	a[4]	p[5]
Active metabolism							
D_{max}	(cm)		35	0.294	0.0133	3.17	0.0001
WSA_b	(cm^2)	body	35	0.682	0.006	5.65	0.0001
WSA_{fp}	(cm^2)	flippers	26	0.488	0.022	1.13	0.0001
WSA_d	(cm^2)	dorsal	26	0.543	0.018	1.84	0.0001
WSA_{ft}	(cm^2)	flukes	26	0.598	0.200	0.46	0.0001
MCD_{fp}	(cm)	flippers	26	0.211	0.015	0.14	0.0001
MCD_d	(cm)	dorsal	26	0.299	0.145	0.06	0.0001
MCD_{ft}	(cm)	flukes	26	0.224	0.021	0.14	0.0001
CL_{fp}	(cm)	flippers	26	0.209	0.030	2.08	0.0001
CL_d	(cm)	dorsal	26	0.285	0.015	1.00	0.0001
CL_{ft}	(cm)	flukes	26	0.194	0.019	2.00	0.0001
Passive heat loss (HL_a)							
MSA_b	(cm^2)	body	35	0.729	0.008	2.76	0.0001
BD_a	(cm)	body	29	0.161	0.026	0.14	0.0001
Energy density							
Fractions of body wet weight							
F_{bl}		Blubber	24	–0.247	0.021	0.32	0.0001
F_m		Muscle	24	0.159	0.012	0.32	0.0001
F_v		Viscera	24	–0.153	0.038	0.24	0.0005
F_{bn}		Bone	24	–0.141	0.022	0.12	0.0001
F_f		Fins	22	–0.239	0.034	0.05	0.0001
Energy densities (mJ/kg dry weight)							
ED_{bl}		Blubber	11	0.021	0.007	33.27	0.0178
ED_m		Muscle	9	–0.041	0.013	25.00	0.0132
ED_{bn}		Bone	5	–0.059	0.050	9.12	0.3248
Water content (% of sample wet weight)							
$\%H_2O_{bl}$		Blubber	11	–0.289	0.085	316.23	0.0067
$\%H_2O_m$		Muscle	10	–0.004	0.007	75.68	0.5956
$\%H_2O_{bn}$		bone	5	–0.191	0.023	331.13	0.0141
Estimated Energy Density							
ED_m	(mJ/kg wet weight)		35	–0.063	0.000	10.21	0.0001

[1]Sample size.
[2]Estimated slope coefficient.
[3]Estimated standard error of slope coefficient.
[4]Estimated intercept for fitted regression.
[5]Significance level (probability).

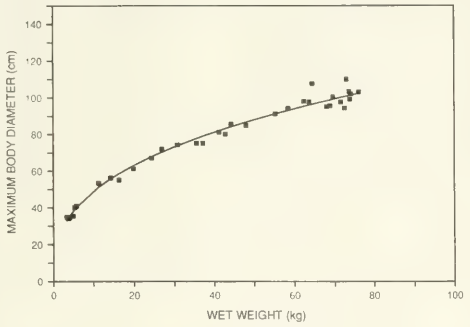

Figure 2

Relationship between **maximum body diameter** (just anterior to dorsal fin; C3 in Fig. 1) and total wet weight of body in kilograms for 35 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Solid line is fitted regression.

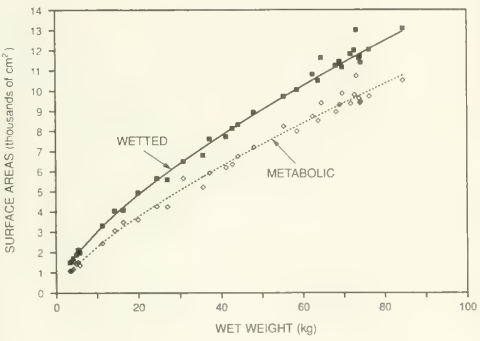

Figure 3

Relationship between **wetted and metabolic surface areas**, and total wet weight of body in kilograms for 35 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

cant trend was found for $\%H_2O_m$ (Fig, 10) or ED_{bn} (Fig. 9). No trends were isometric (linear) in the untransformed variables. Trends fell into three general groups based on the strength of the relationship between parameter value and wet weight (Table 4). Expressed in terms of the regression coefficient (b), these relationship groups were strong ($0.49 < b < 0.73$), intermediate ($-0.29 < b < -0.14$ or $0.16 < b < 0.30$), and weak ($-0.14 < b < 0.16$). Strong trends were found for all five of the surface area measurements (MSA_b, WSA_b, WSA_{fp}, WSA_d, WSA_{fl}; Figs. 3 and 4). Weak trends were found for energy densities of blubber and muscle (ED_{bl}, ED_m; Fig. 9). Intermediate trends represented the majority of the relationships (16 of 25) and included D_{max} (Fig. 2), all measures of MCD (Fig. 5), CL (Fig. 6), BD_a (Fig. 7), F (Fig. 8, A and B), $\%H_2O_b$ and $\%H_2O_{bn}$ (Fig. 10), and ED_{an} (Fig. 11).

Parameters that exhibited strong trends demonstrated large changes in parameter values throughout the weight range studied. Although the allometric effect decreased somewhat with increasing size, parameter estimates were 300–400% larger for 30-kg than for 5-kg dolphins (compared with a difference of 600% (30 kg/5 kg*100) in wet weight), and 50%–85% larger for 70-kg than for 30-kg dolphins (compared with a difference of 233% in wet weight; Table 4).

Parameters showing intermediate trends changed rapidly only from birth through the first 2–3 years of life (5–30 kg; Perrin et al., 1976; Hohn and Hammond, 1985). Parameter values changed much more slowly with size in older (larger) dolphins (30–70 kg) than in smaller dolphins (e.g., less than 30 kg). For example, estimated muscle fraction of body wet mass increased by 33% from 5-kg to 30-kg dolphins, but only by 14% from 30 to 70 kg wet weight (Table 4). Parameter estimates for these intermediate effects differed from 10% to 70% between 5- and 30-kg dolphins, but only from 5% to 30% between 30- versus 70-kg dolphins (Table 4).

Parameter values showing weak trends changed little with increasing size. For example, estimated ED_m increased only 8% in animals 5 kg to 30 kg in weight, and only an additional 4% from animals 30 kg to 70 kg in weight (Table 4). The lack of any significant trend in ED_{bn} may be due to small sample size ($n = 5$ animals) but the relatively small scatter of the existing points indicates that the apparent absence of trend is probably real (Fig. 9). The lack of trend in H_2O_m also appears real, as sample size was reasonably large ($n = 10$) and scatter about the regression line relatively small (Fig. 10).

Discussion

Estimates for individual dolphins

The practical importance of any allometric trend in any particular parameter will depend not only on the strength of the trend, but also on that parameter's relative contribution to the energy flux being estimated. This contribution is affected by the algebraic placement of the parameter in the energy flux calculation,

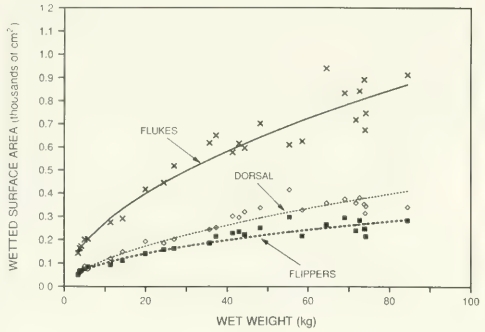

Figure 4

Relationship between **wetted surface areas of fins** and total wet weight of body in kilograms for 26 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Areas are total for both sides of dorsal, both sides of both flippers, and both sides of both flukes. Lines through points are fitted regressions.

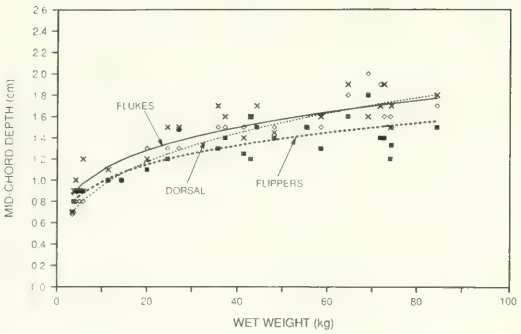

Figure 5

Relationship between **mid-chord depths of fins** and total wet weight of body in kilograms for 26 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

by the actual values taken on by the parameter, and by the relative importance of the energy characteristic in the overall energy budget.

For example, the relative importance of the parameters WSA_b and D_{max} in the equation for active metabolism is highly dependent on both parameter placement and relationship with wet weight (trend). Active metabolism (cal·hr^{-1}) can be estimated for steady submerged swimming by torpedo-shaped bodies as

$$ACT = 20650 * MP/(ME*PE),$$

where
$$ME = 0.20$$
$$PE = 0.85$$
$$MP = ((D_T/1e^7) * VL)$$
$$D_T = (0.5 * N * VL^2 * WSA_b * C_T) / (1.0 - FID)$$
$$N = (1.025\ \text{g/cm}^3)$$
$$FID = 0.21$$
$$C_T = C_f * [1 + (1.5*((D_{max})/\text{TL}))^{3/2} + (7*((D_{max})/\text{TL}))^3]$$
$$C_f = 0.072\ R_L^{-1/5}$$
$$R_L = (TL * VL)/\upsilon$$
$$\upsilon = 0.01\ \text{Stokes}$$

VL is velocity (cm.sec^{-1}) and TL is total length in centimeters (Edwards, 1992, following Webb, 1975).

Collecting and assuming constant all terms except the energetics parameters WSA_b and D_{max}, the expression for active metabolism can be simplified to

$$ACT = C * WSA_b * [1 + (1.5*((D_{max})/\text{TL}))^{3/2} + (7*((D_{max})/\text{TL}))^3],$$

where C represents the collected terms.

The effects of increasing or decreasing the values used for WSA_b and D_{max} can be seen more readily in this formulation. Changes in the value of WSA_b lead directly to equivalent changes in the estimate of ACT (e.g., increasing WSA_b by 50% will increase the estimated cost of activity by 50%). WSA_b not only has a direct effect on estimates of activity cost, but has also a strong relationship with wet weight, leading to differences of up to 80% in estimates of activity costs for 30-kg versus 70-kg spotted dolphins (WSA_b for a 70-kg dolphin is 78% larger than for a 30-kg dolphin, Table 4). Differences are near 350% for 5-kg versus 30-kg dolphins (WSA_b for a 30-kg dolphin is 339% greater than for a 5-kg dolphin, Table 4).

Conversely, changes in D_{max} have little actual effect on activity estimates, both because changes with size are smaller overall and because of the parameter's algebraic placement in the equation for activity costs. The ratio D_{max}/TL will always be quite small (e.g., 5/80 = 0.065 in an 80-cm dolphin (D_{max} = 5 cm) weighing 5 kg; 11/210 = 0.052 in a 210-cm dolphin (D_{max} = 11 cm) weighing 70 kg). Because this small term is made even smaller by raising it to higher powers, changes in D_{max} will have little effect on estimates of ACT (e.g., doubling D_{max} from 5 to 10 cm for an 80-cm dolphin

changes the value of the term in brackets only from 1.03 to 1.08). This lack of effect occurs despite the fact that D_{max} has an intermediate-level relationship with wet weight (Table 4).

Examining the placement of MSA_b and BD_a in the equation for passive heat loss also illustrates that their relative importance is highly dependent on both parameter placement and relationship with wet weight. Passive heat loss can be estimated as (Edwards, 1992, following Brodie, 1975).

$$H_u = \frac{((21.18/BD_a) * (37.0 - T_a) * MSA_b/10000.0) * 24}{WW_g * (CD_d/1000.0)}.$$

Collecting and assuming constant all terms except the energetics parameters BD_a and MSA_b,

$$H_u = (MSA_b/BD_a) * C,$$

where C represents the collected terms.

Once again, changes in the surface area measurement (MSA_b) will lead directly to equivalent changes in estimates of HL_u, and the strong relationship between MSA_b and wet weight will be readily reflected in the estimates. However, unlike the case for D_{max}, changes in values used for BD_a will have a significant (reciprocal) effect on estimates of HL_u (e.g., increasing blubber depth by 30% [i.e., by a factor of 1.30] will decrease the estimate for H_u by about 23% [1/1.30 = 0.77]) owing to the difference in the way the parameter is expressed in the equation. In this case, the intermediate-level relationship of BD_a with wet weight *will* be reflected in the estimate of energy flux.

Allometric effects in parameters related to bone provide an example of largely irrelevant, though statistically significant, trends. The bone fraction of body weight is small (about 10%: Fig. 8A), and its energy density low (less than 1/4 the energy density of blubber, 1/3 the energy density of muscle). Given no indication from the energy densities in the small sample studied that spotted dolphins store lipid within the skeleton, even relatively large changes with size will have little effect on whole-animal energy calculations. Even though the fraction of body weight due to bone has an intermediate-level relationship with wet weight, decreasing 30% from 5-kg to 30-kg dolphins, the decrease in terms of total body weight is only from 10% to 7% (Table 4).

Thus, the practical importance of any allometric trend depends on other factors in addition to actual strength of the trend with wet weight, but in general for spotted dolphins, these trends are expressed primarily during the first two or three years of life (5-30 kg wet weight). Parameter estimates for small

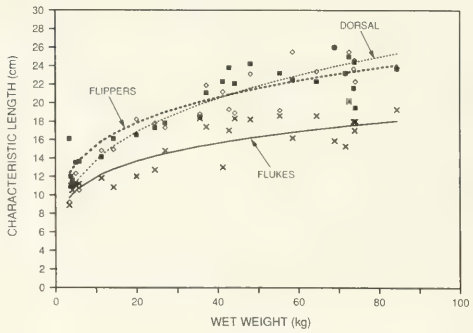

Figure 6

Relationship between **characteristic lengths of fins** and total wet weight of body in kilograms for 26 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

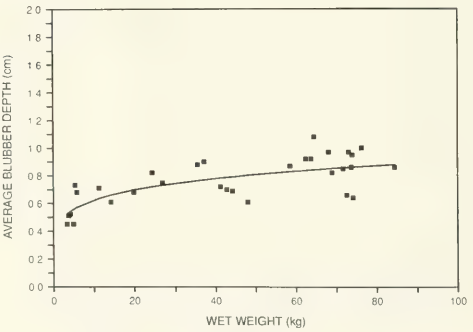

Figure 7

Relationship between **average blubber depth** and total wet weight of body in kilograms for 29 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

dolphins (less than about 30 kg wet weight) should be derived from measurements on animals near the specific size of interest. Estimates for larger animals, with the exception of the surface area measurements, could be estimated reasonably well from any specimens greater than about 30 kg wet weight.

Population energetics

The examples presented above pertain to estimates for individual spotted dolphins. Implications of allo-

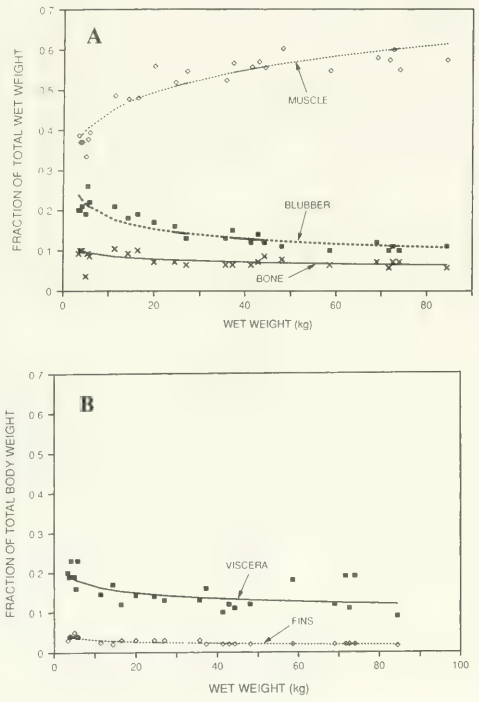

Figure 8

(A) Relationship between fractions of total body wet weight comprising **muscle, blubber, and bone**, and total wet weight of body in kilograms for 24 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions. **(B)** Relationship between fractions of total body wet weight comprising **viscera and fins**, and total wet weight of body in kilograms for spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

metric trends for estimates of population energy flux are not necessarily straightforward. Dolphins less than about 3 years old represent only about 10% of the population in these relatively long-lived and slowly reproducing mammals; dolphins age 3–12 compose about 40% and sexually mature adults about 50% of the population (Barlow and Hohn, 1984; Hohn and Hammond, 1985). Because they are so few and because their biomass is so small, ignoring allometric effects when estimating energy fluxes for the younger animals, or ignoring the younger animals altogether, will have little direct effect on population energy budgets.

However, the indirect effects may be considerable. To the extent that activities of older animals are constrained by energy-related characteristics of young dolphins, indirect effects of size-related differences in estimated energy fluxes may be more important than the absolute fluxes themselves, through regulating behavior or ecological relationships. For example, muscle fraction of body mass in neonate dolphins (5 kg) is about 30% less than the muscle fraction in adults (70 kg; Figure 8A, Table 4). Thus the power available for swimming (as a function of muscle mass) is 30% less than would be estimated based on measurements from adult animals. The estimated speeds that small dolphins, with their smaller muscle mass, can maintain will be slower than speeds estimated by simply applying to neonates parameter values derived from adults.

Differences in estimated swimming speed may be important because dolphins are schooling mammals with apparently strong social ties and prolonged periods of parental care for nursing offspring. In order to remain within the same school, the average speed for all individuals will be constrained to the slower speeds that can be maintained by smaller dolphins. Estimates from tagging studies of spotted dolphins in the ETP indicate that in fact the average cruising speed of dolphin schools is the optimum for neonates rather than for adults, despite the fact that adults represent the majority of individuals in the schools (Edwards, 1992, and references therein). Using parameters appropriate for adult dolphins in estimates for the smaller animals would produce unreasonably high estimates of sustainable power output (and therefore food consumption) by the smaller animals (Edwards, 1992). School speeds, and therefore energy requirements to maintain these speeds, may thus be constrained by energetics characteristics of small animals that cannot be extrapolated simply from measurements on adults. As cost of transport is a large fraction of the total energy requirements of a swimming mammal (active metabolism in swimming homeotherms [including dolphins, sea otters, and penguins] is generally 2 to 3 times that of resting metabolic rates [Hui, 1987]), maintaining reduced speeds should reduce energy costs and therefore forage requirements for the school moving as a unit. This is particularly significant because forage requirements are the most commonly estimated energy flux used to estimate the impact of a

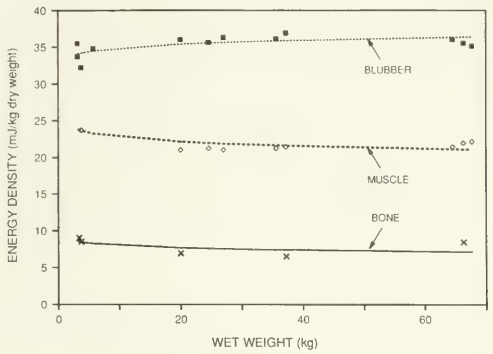

Figure 9

Relationship between **energy density** (per gram dry weight) of blubber (11 specimens), muscle (9 specimens) and bone (5 specimens), and total wet weight of body in kilograms for spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

Table 4

Predicted values and fractional differences (ratios) between those values for energetics parameters showing strong, intermediate, and weak allometric effects, for spotted dolphins weighing 5, 30, and 70 kg wet weight. Regression coefficient indicated by (b).

	Predicted values			Ratios	
	5 kg	30 kg	70 kg	30 kg/5 kg (6.0)	70 kg/30 kg (2.3)
Strong relationship (b>0.49)					
MSA_b	8.92	32.94	61.09	3.69	1.85
WSA_b	16.93	57.47	102.42	3.39	1.78
WSA_m	2.48	5.94	8.98	2.40	1.51
WSA_d	4.41	11.67	18.48	2.65	1.58
WSA_{fl}	1.20	3.52	5.84	2.92	1.66
Intermediate relationship (–0.14<b<–0.29 or 0.16<b<0.30)					
D_{max}	5.09	8.62	11.05	1.69	1.28
MCD_m	0.20	0.29	0.34	1.46	1.20
MCD_d	0.10	0.17	0.21	1.71	1.29
MCD_{fl}	0.20	0.30	0.36	1.49	1.21
CL_m	2.91	4.23	5.05	1.45	1.19
CL_d	1.58	2.64	3.36	1.67	1.27
CL_{fl}	2.73	3.87	4.56	1.42	1.18
BD_a	0.20	0.26	0.29	1.29	1.13
F_{bl}	0.22	0.14	0.11	0.64	0.81
F_m	0.41	0.55	0.63	1.33	1.14
F_t	0.19	0.14	0.13	0.76	0.88
F_{bn}	0.10	0.07	0.07	0.78	0.89
F_r	0.03	0.02	0.02	0.65	0.82
H_2O_{bl}	198.61	118.34	92.63	0.60	0.78
H_2O_{bn}	243.50	172.93	147.09	0.71	0.85
ED_{an}	9.23	8.24	7.81	0.89	0.95
Weak or insignificant relationship (–0.29<b<0.16)					
ED_{bl}	34.41	35.73	36.37	1.04	1.02
ED_m	23.40	21.75	21.00	0.93	0.97
ED_{bn}	8.29	7.46	7.10	0.90	0.95
$\%H_2O_m$	75.19	74.66	74.40	0.99	1.00

cetacean population preying on a fisheries resource (e.g., Overholz et al., 1991).

The practical significance of these results for a given population's estimates will depend on values chosen for a number of parameters in addition to those presented here (e.g., ambient temperature, average swimming speed, size composition of the population). Such calculations are beyond the scope of the present study, but these results for spotted dolphins from the ETP show that allometric trends should be considered in such calculations. Similar effects probably occur in other cetacean populations and should be investigated.

Caveats

The regressions presented here include data from a number of "neonate" dolphins which were actually late-term fetuses rather than true neonates. Specimens of true neonates are rare. But the relatively smooth fit through data collected from near-term fetuses and first to third-year juveniles imply that the physical characteristics predicted for the under-sampled size ranges from 5–30 kg wet weight, if one uses the regressions presented here, are likely to be accurate.

The large water content of bone and blubber in fetal specimens probably reflects conditions that change rapidly after birth, when fetal nutrition changes from placental to milk-derived. It is not possible with the present data set to identify exactly how quickly water content decreases. However, errors in energetics estimates resulting from inaccurate estimates of bone water content will be negligible owing to the relatively small contribution made to energy flux by skeletal materials. Errors in estimates of water content of blubber for spotted dolphins in the weight range 5–30 kg wet weight could be more serious. Although the true extent of the problem cannot be determined from this data set, possible values for this size range vary from about 15% to 30% (Fig. 10).

Changes in maternal body composition (and thus energetics estimates) during pregnancy and lactation may occur in spotted dolphins as they do in large whales (Lockyer 1981, a and b) but such changes, if they occur, are apparently much more subtle in spotted dolphins from the ETP. No dramatic differences in body fractions or energy density of blubber or muscle were discernable in the set of specimens analyzed during this study, which were collected from a variety of times and places. It is unlikely that major changes occur in

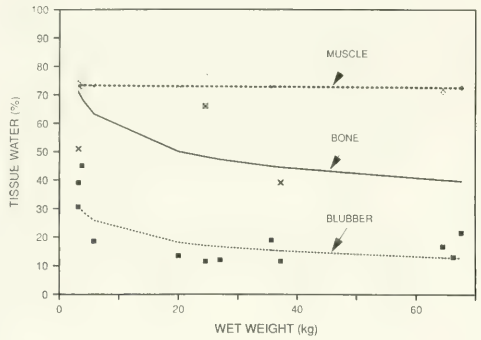

Figure 10

Relationship between **water content** of muscle, blubber and bone vs. total wet weight of body in kilograms for spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

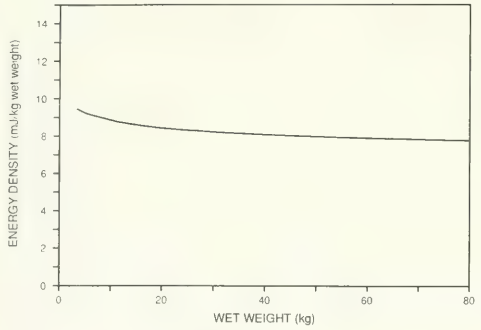

Figure 11

Estimated relationship between **total energy density** and total wet weight of body in kilograms for spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented.

spotted dolphins, as these small cetaceans appear to reside continually within the *relatively* constant (compared to temperate and polar regions) environment of the eastern tropical Pacific Ocean (Fiedler, 1990). There is apparently little need for these animals to develop and sequester significant energy reserves and insulation for conducting lengthy migrations to or through areas of little food, or through areas of cold water.

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Harbor Porpoise, *Phocoena phocoena* (L.), in the coastal waters of northern Japan

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Abstract.–Little is known of the distribution, life cycle, and status of the harbor porpoise *Phocoena phocoena* in the northwestern Pacific Ocean and adjacent seas. In the present study we assess information in the literature and re-examine 15 specimens in the National Science Museum, Tokyo, in conjunction with data from 45 new animals collected from a variety of sources between 1983 and 1989. Maximum recorded lengths of harbor porpoises from Japanese waters are 158 cm for males, and 185 cm for females, and maximum age was 11 years. All females exceeded the average length of North Sea females at given ages. Size at birth is probably about 80 cm, and parturition likely occurs in May–June in northern Japanese waters, as in the North Atlantic. Known and historical geographical limits are given and compared with the equivalent habitat conditions extant in the western North Atlantic. The most southerly winter record is from Taiji, Wakayama, at latitude 34°15'N and the most northerly confirmed sighting from Shelikhova Bay in the northeastern Sea of Okhotsk at 57°–58°N, in August 1989. The latter is unlikely to represent the northern limit of the summer-fall distribution. Seasonal migrations, especially in and out of the Sea of Okhotsk, must occur because of extensive ice coverage in winter, but in Japanese waters there are confirmed records of porpoises as far north as the northern tip of Hokkaido Island in January.

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Harbor porpoises, *Phocoena phocoena*, are confined to the northern hemisphere; a near-circumpolar distribution is found in temperate latitudes (Tomilin, 1957; Gaskin, 1984). Although most often sighted in coastal waters, they also occur over adjacent offshore banks, and sometimes over deep water (Jones, 1984; Stenson and Reddin, 1990). There are populations around relatively isolated land masses, such as Iceland, and harbor porpoises also occur in subarctic and arctic waters, especially in summer months (Van Bree et al., 1977).

Interest in the harbor porpoise has increased significantly in recent years and Hohn and Peltier (1990) published a useful bibliography of articles on this species, although detailed life history and distributional data are still sparse in many regions. Population surveys and life history studies of the harbor porpoise have been concentrated in the coastal waters of western Europe, the northwestern Atlantic, and northeastern Pacific. Some pertinent references are the following but the list is not exhaustive: **Western Europe**: Møhl-Hansen (1954), Fraser (1974), Noldus and de Klerk (1984), Kinze (1985, 1990a, 1990b), Anderson (1990), Bjorge and Kaarstad (1990), Bjorge and Oien (1990), Evans (1990), and Sequiera (1990); **Black Sea**: Zalkin (1940), Tomilin (1957) and Celikkale (1990). **Northwestern Atlantic**: Fisher and Harrison (1970), Gaskin (1977, 1984), Gaskin and Blair (1977), Prescott and Fiorelli (1980), Kraus et al. (1983)[1], Gaskin et al. (1984), Gaskin and Watson (1985), Yurick and Gaskin (1987), Polacheck (1990), Polacheck and Wenzel (1990), Read (1990, a and b), Fontaine et al. (1991), Read and Gaskin (1990); **Northeastern Pacific**: Flaherty and Stark[2], Taylor and Dawson (1984), Hannan et al.[3], Barlow (1988), Barlow et al. (1988),

[1]Kraus, S. D., J. H. Prescott, and G. S. Stone. 1983. Harbor porpoise, *Phocoena phocoena*, in the U.S. coastal waters of the Gulf of Maine: A Survey to determine seasonal distribution and abundance. Report to the Director, National Marine Fisheries Service, Northeast Region, Woods, MA, 15 p.

[2]Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound." NOAA, NMFS, National Marine Mammal Laboratory, Seattle, WA, Final Rep. for Subcontract 80-ABA-3584.

[3]Hanan, D. A., S. L. Diamond and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California set net fisheries April 1, 1984 through March 31, 1986. National Marine Fisheries Service, Southwest Region, Terminal Island, CA, Admin. Rep. 5WR-86-16, 38 p.

Barlow and Hanan (1990), Hohn and Brownell (1990), Dalheim et al. (1991), Forney and Barlow (1991), Rosel and Haygood (1991) and Stacey et al. (1990).

The life history of the harbor porpoise has been well studied in the North Atlantic and northeastern Pacific, but little is published about the distribution, movements and life history of the species in the waters of Japan and adjacent regions of eastern Russia. Jones (1984) recorded 10 specimens taken incidentally in salmon nets from 1978 to 1981 near the eastern Aleutians and one male at 57°N some 700 miles east of central Kamchatka. Miyashita and Doroshenko (1990), and Miyashita and Berzin (1991) reported a few recent summer sightings of harbor porpoises in the northeastern and northwestern Sea of Okhotsk and between southeastern Sakhalin and the southern Kurile Islands. Earlier, Nishiwaki (1966) concluded that the harbor porpoise was less common off Japan than in North American waters. Ohsumi (1972), however, regarded it as common around northern Japan, including the northern Pacific coast of Honshu, and Hokkaido; Hawley (1960) noted it was taken incidentally in the herring fishery in this region. Some catches of harbor porpoise have been reported (Table 1) in Japanese coastal fisheries statistics provided to the International Whaling Commission (1984, 1985, 1986, 1987, 1988, 1989, 1990) and by Miyazaki (1983), but identifications in the catch statistics are not always reliable and could include some Dall's porpoises[4]. Miyazaki et al. (1987) made preliminary comparisons of growth and skull morphology of Japanese porpoises with samples from the North Atlantic and northeastern Pacific. Recently Amano and Miyazaki (1992) repeated the analyses of skull morphology with larger samples and compared their results with those of Yurick and Gaskin (1987), using more sophisticated analysis than Miyazaki et al. (1987).

The harbor porpoise is now considered to be seriously threatened in several parts of the world, for example in the Baltic Sea, Black Sea, and Bay of Fundy—Gulf of Maine, where indirect and direct catches (Hohn and Peltier, 1990) may have contributed to dramatic declines in numbers in recent years (IWC, 1984; Read and Gaskin, 1990; Gaskin, 1992). Given the high fishing effort involving gill nets and trap nets in Japanese coastal waters (Tobayama et al., 1991) and the dearth of data for the harbor porpoise population in this region, any new information is useful. A systematic assessment of the status of the species around Japan would be desirable.

The objective of the present study was to increase the data base for harbor porpoise in Japanese waters. We collected new material; examined and measured harbor porpoises in Oceanaria; and verified documented but unpublished captures and stranding records from museums, fisheries institutions and other agencies in Japan. We tabulate data from 45 new specimens, together with the 15 originally examined by Miyazaki et al. (1987). We present for the first time, the apparent changes in seasonal distribution of the harbor porpoise in the waters of Japan and adjacent regions. We combine and re-analyze the new data in conjunction with those published by Miyazaki et al. (1987) to improve insights into the life history of harbor porpoise in the region. We reinforce the length-age relationships reported by Miyazaki and his colleagues and estimate the length at birth, and probable season of parturition of harbor porpoises in northern Japanese waters.

Table 1

Summary of reported catches of harbor porpoises in Japanese waters, taken from domestic fisheries statistics incorporated in national progress reports on cetacean research (IWC 1984–1990).

Year of capture	Months	Locations	Numbers	Annual totals	Gear	Year of IWC volume
1983	[1–12]	Iwate Pref.	20	20	Hand harpoon[1]	(1985)
1984	—	Hokkaido	6		Gillnets	(1986)
	—	Hokkaido	30	36	Pound nets	
1985	[1–12]	Iwate Pref.	55		Pound nets	(1987)
	[6–8]		1		Pound nets	
	[6–12]	Hokkaido	1	66	Gillnets	
1986	[6–9]	Hokkaido	30		Hand harpoon[1]	(1988)
	[4–9]	Hokkaido	36	66	Pound nets	
1987	[4–12]	Hokkaido	17		Pound nets	(1989)
	[1–12]	Nagasaki	4	21	Pound nets[1]	
1988	—	No breakdown	71		Gillnets	(1990)
		by region given	6	77	Hand harpoon[1]	

[1]Specific identification particularly doubtful. Because of the level of uncertainty about identifications of animals taken in the hand harpoon fishery, the totals reported for each year should be cited with caution. We also note the following known omissions: 1983: 1 more from Hokkaido gill nets; 1984: 2 more from northern Honshu pound nets; 1985: 21 more from Hokkaido gill nets and pound nets. These are not included in the body of the table to avoid potential confusion with the officially reported statistical data.

[4]Toshio Kasuya, Far Seas Fisheries Research Laboratory, Shimizu, Shizuoka, Japan, pers. commun. 1985.

Materials and methods

We re-examined the 15 harbor porpoise specimens in the collection at the National Science Museum in Tokyo, and obtained data on 45 new specimens, bringing the total sample size to 60. One of us (A.K.) encouraged local fishing companies and the Oceanaria in Hokkaido and northern Honshu to collect, sex, measure and preserve specimens or designated samples (e.g., teeth, testes, ovaries, and pieces of blubber) of *Phocoena phocoena*, killed in fishing gear from 1983 onwards. This program yielded 12 animals, mostly from gill nets. In April and May of 1985 and 1986, the authors arranged frequent inspections of the floating pound nets operated by the Nomura Fishing Company of Usujiri, Hokkaido, which are set to catch tuna, squid, and salmon, depending on the season. Salmon are the target species during April and May. From these nets we collected another 16 specimens: 11 in 1985 and five in 1986. During the same period we were invited to the three Oceanaria which held captive harbor porpoises, Otaru Aquarium in western Hokkaido, Asamushi Aquarium in Aomori, northern Honshu and Sunshine City Aquarium in Tokyo. We obtained measurements and body weights of 14 live or frozen specimens in these facilities. Additional confirmed records of three more stranded specimens, presently with few data, were obtained by A.K. through telephone conversations, and descriptions, from Noshiro (February 1987, sex unrecorded), Niigata (February 1989, ♂) and Nishiyama (March 1987, sex unrecorded) (Fig. 1). All measurements of porpoises were made to the nearest 0.5 cm and weights to the nearest 0.1 kg.

Causes of entrapment were known in almost all cases (Tables 1 and 2). Ages are now known for 28 animals, 14 males and 14 females, of which ages of 6 males and 9 females were determined by Miyazaki et al. (1987). Age determinations of newly acquired specimens were made from thin longitudinal sections of dentine according to the methods of Gaskin and Blair (1977). Ages of the National Science Museum specimens were estimated from decalcified sections by Miyazaki et al. (1987), based on both dentine and cementum layers in each specimen.

The reproductive status of males was determined by using the criteria of Gaskin et al. (1984): 1) Immature, ie. single testis volume much less than 90 cc; and 2) Mature but inactive, ie. single testis volume greater than 90 cc but with no seminal fluid present in the seminiferous tubules or epididymis. No mature males were taken with testes in an active state.

Female porpoises were classified as mature if one or more corpora albicantia or a corpus luteum were present, or immature if none could be found, again according to Gaskin et al. (1984).

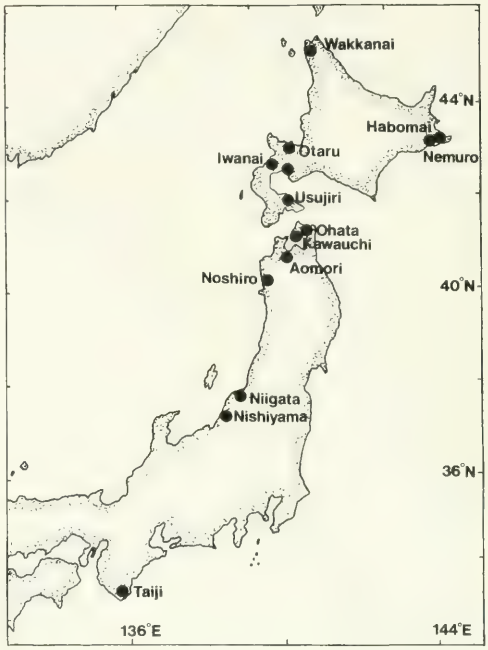

Figure 1
Localities of confirmed harbor porpoise records in Japan, as listed in Tables 2 and 3.

A few collections of stomach contents were obtained from the porpoises killed in fishing gear and were preserved in 70% ethyl alcohol.

All materials obtained during this study have been lodged at Hokkaido University (Hakodate campus) and the National Science Museum, Tokyo.

Results

Japanese localities used in the text are shown in Figure 1. Location, date of capture, lengths, body weights, age and reproductive condition are given in Table 1 for males and Table 2 for females. Specimens previously examined by Miyazaki et al. (1987) are clearly distinguishable by the National Science Museum collection prefix (M-)[5].

[5]One male, M2490 from Nemuro, was not used by Miyazaki et al. (1987).

Table 2

Summary of basic data of male harbor porpoises, *Phocoena phocoena*, from Japanese waters, 1977–86, including specimens examined by Miyazaki et al. (1987), which are identified by the National Science Museum Prefix (M-). Localities shown in Fig. 1.

Year	Date	Body length (cm)	Body weight (kg)	Age (yr)	Reprod. cond.	Collection no.	Locality/ fishing gear
1977	31 May	120.5	32.0	2.0	Im[1]	M24961	Habomai, Hokkaido
	— May	161.5	64.0	3.0	—	M27387	Habomai, Hokkaido
	08 Dec.	127.0	30.2	2.0	Im	M24960	Nemuro, Hokkaido
	12 Dec.	118.0	—	—	Im	M24959	Nemuro, Hokkaido
1983	01 Jan.	126.0	26.5	—	Im	85.28	Wakkanai, Hokkaido gill net
	22 Apr.	149.0	34.8	—	Mt[2]	85.11	Ohata, Honshu pound net[3,4]
1984	06 Mar.	158.0	60.0	7.0	Mt	85.16	Kawauchi, Honshu[3,4]
	19 Apr.	145.5	41.0	8.5	—	M27139	Usujiri, Hokkaido pound net
	20 Apr.	117.0	25.0	2.0	Im	M27140	Usujiri, Hokkaido pound net
	14 May	132.0	40.0	—	Im	85.17	Aomori, Honshu gill net
	29 May	127.0	23.0	—	Im	85.15	Usujiri, Hokkaido pound net[3,4]
1985	21 Jan.	142.0	—	—	—	85.19	Otaru, Hokkaido gill net
	17 Mar.	120.0	—	—	Im	85.20	Iwanai, Hokkaido gill net
	13 Apr.	129.0	31.5	—	Im	85.14	Usujiri, Hokkaido pound net[5]
	04 Apr.	147.5	37.3	7.0	Mt	85.02	Usujiri, Hokkaido pound net
	04 Apr.	157.0	—	—	Mt	85.22	Otaru, Hokkaido octopus hook trap
	13 Apr.	134.0	41.0	—	—	85.12	Usujiri, Hokkaido pound net[5]
	28 Apr.	145.5	31.0	8.0	Mt	85.18	Usujiri, Hokkaido trap net
	30 Apr.	139.0	36.0	-		85.26	Usujiri, Hokkaido pound net[3,6]

Table 2 (Continued)

Year	Date	Body length (cm)	Body weight (kg)	Age (yr)	Reprod. cond.	Collection no.	Locality/ fishing gear
1985	30 Apr.	112.0	23.4	1.0	Im	85.04	Usujiri, Hokkaido pound net
	01 May	121.0	32.8	1.0	Im	85.07	Usujiri, Hokkaido pound net
	01 May	149.5	46.9	11.0	Mt	85.08	Usujiri, Hokkaido pound net
	05 May	139.0	31.1	3.0	Mt	85.05	Usujiri, Hokkaido pound net
	15 May	123.0	—	—	Im	85.10	Usujiri, Hokkaido pound net
	15 May	129.0	24.3	2.0	Im	85.09	Usujiri, Hokkaido pound net
	17 May	134.0	40.0	—	—	85.23	Shizukari, Hokkaido pound net[3,6]
	24 May	119.0	33.0	—	Im	85.24	Shizukari, Hokkaido pound net[3]
1986	03 Mar.	30.0		0	Fetus	86.06a	Otaru, Hokkaido mother in gill net
	03 Mar.	144.0	45.0	—	Mt	86.05	Otaru, Hokkaido gill net
	05 Mar.	135.0	37.0	—	—	86.08	Otaru, Hokkaido gill net
	14 Apr.	138.0	37.0	—	—	86.10	Usujiri, Hokkaido pound net[3]
	24 Apr.	124.0	26.6	—	Im	86.01	Usujiri, Hokkaido pound net
	24 Apr.	58.5	3.7	0	Fetus	86.02a	Usujiri, Hokkaido mother in pound net
Unknown		133.5	45.0	3.0	—	M27392	Nemuro, Hokkaido

[1]Im (Immature).
[2]Mt (Mature).
[3]Live to Otaru Aquarium, Otaru.
[4]Died later in captivity.
[5]Live to Asamushi Aquarium, Aomori.
[6]Transferred from Otaru Aquarium to Tokyo.

Males

Including those examined by Miyazaki et al. (1987), males ranged in length from 112 cm to 161.5 cm (N = 34); in addition, two male fetuses of 30 cm and 58.5 cm were obtained. Ages were determined for 14 animals, based on one growth layer group (GLG) per annum (Gaskin and Blair, 1977; Miyazaki et al., 1987; Watts and Gaskin, 1989) and ranged from one (112–121 cm, N = 2), 2 (117–129 cm, N = 4), 3 (133.5–161.5 cm,

$N = 3$), 7 (147.4, 158 cm, $N = 2$), 8 (145.5 cm, $N = 2$), to 11 (149.5 cm, $N = 1$) (Table 2). Testis samples were available for eight mature males of known age. All were captured in March, April or May, 1983–1986, and all specimens had inactive testes.

Females

Including those examined by Miyazaki et al., 1987), females ranged in length from 92.4 to 185 cm ($N = 25$); in addition, one fetus of 62 cm was obtained. Ages were determined for 14 specimens, ranging through 0.5 (92.4 cm, $N = 1$), 2–2.5 (121–143.5 cm, $N = 6$), 3 (131.5–140 cm, $N = 3$), 4 (140 cm, $N = 1$), 8–8.5 (162–166 cm, $N = 2$) to 9 years (173 cm, $N = 1$) (Table 3). Seven animals were mature, with one or more corpora albicantia. Four of these specimens were pregnant, but none were lactating, based on the non-distended nipples and gross sections of mammary gland which revealed no traces of milk.

Fetuses

These were collected on 03 March 1986 (30 cm, $N = 1$) by the Otaru Aquarium (one other was not retained and not measured), at Otaru on the west coast of Hokkaido, and on 24 April 1986 (58.5, 62 cm, $N = 2$), at Usujiri on the Pacific coast of southern Hokkaido. Miyazaki et al. (1987) recorded a 73 cm fetus on 3 May 1986, from a female taken at 42°37'N, 144°28'E.

Immature animals of both sexes

Samples (Tables 2 and 3) from Wakkanai, Nemuro, Habomai, Aomori, Usujiri, Shizukari, Iwanai, and Taiji and in all months sampled other than March (January, April, May, October, and December) showed evidence of immature animals of both sexes. All were ≤143.5 cm in length ($N = 25$). Although seven animals were collected from Otaru in March and one in April, there were no immature animals in the samples.

Length-Age relationships

Miyazaki et al. (1987) plotted the age/length relationships of nine males and six females from Japanese waters against those from other regions. We have replotted these data (Fig. 2), incorporating the new specimens obtained in the present study, giving a total 28 specimens (14 males and 14 females) of known age from Japanese waters. The small samples and clustering still preclude valid statistical comparison and legitimate calculation of age-length curves, but female porpoises from Japan are still shown to be larger than females from the North Sea at given ages, as Miyazaki et al. (1987) observed.

Stomach contents

We examined the stomachs of 16 porpoises from trap nets near Usujiri and were given samples from four more taken from gill nets by staff at the Otaru Aquarium near Otaru, in April–May of 1985 and 1986. Fifteen stomachs were nearly empty. All contained varying numbers of round worms, *Ascaris* spp. A small quantity of seaweed was found in one 129 cm male; a large quantity of seaweed and a 1-m length of 0.25 cm fishing gear twine were found in a 139-cm male in poor condition (sunken dorsal musculature and blubber only about 1 cm in thickness). The twine was caught distally at the entrance to the oesophagus and stretched into the second stomach compartment. Food items in the remaining five porpoises were similar. They included small squid beaks (probably Ommastrephidae) and eroded otoliths in varying quantities, tentatively identified as herring *Clupea* sp., anchovy *Engraulis* sp., and hake *Merluccius* sp. The condition of the remains was poor, and because stomach contents from porpoises from trap nets probably represent only coincident prey trapped with them, we do not report these items in detail.

Discussion

Body length at birth and probable season of parturition

Lengths of three fetuses collected from females caught off Japan were compared with fetal growth curves from the western and eastern Atlantic populations (Fig. 2 in Gaskin, 1984). Their lengths fell on or just above the growth curves for Atlantic porpoises. Length at birth in the Hokkaido population, therefore, is probably close to 80 cm, and parturition in northern Japanese waters is probably in May–June, judged not only by comparison with the neonatal growth curve of Gaskin et al. (1984) and coincident length/month relationship but also by the parallel degree of development of the fetuses examined from Usujiri and the North Atlantic.

Life history pattern

Based on published literature, there is considerable synchrony in the seasonal breeding of the harbor porpoise throughout its range (Gaskin, 1984). From the limited data presently available from Japanese waters (eg., sizes of fetuses in spring and state of mature testes), we expect the timing of the cycle in the northern Japanese population to be similar to the North

Table 3

Summary of basic data of female harbor porpoises, *Phocoena phocoena*, from Japanese waters collected 1973–86, including specimens examined by Miyazaki et al. (1987), which are identified by National Science Museum Codes (M-). Localities shown in Fig. 1.

Year	Date	Body length (cm)	Body weight (kg)	Age (yr)	Reprod. cond.	Collection no.	Locality/ fishing gear
1973	27 Jan.	135.0	30.0	2.0	Im	M24902	Taiji, Wakayama Honshu
1977	14 Oct.	131.5	38.0	3.0	Im	M24958	Nemuro, Hokkaido
	— May	137.6	36.0	2.0	Im	M27389	Habomai, Hokkaido
	— May	140.2	—	3.5	—	M27388	Nemuro, Hokkaido
	— May	143.5	48.0	2.5	Im	M27890	Habomai, Hokkaido
1984	17 May	129.0	35.0	2.0	Im	M27141	Usujiri, Hokkaido
1985	23 Mar.	143.0	—	—		85.21	Otaru, Hokkaido gill net
	04 Apr.	138.0	38.6	3.0	Mt	85.01	Usujiri, Hokkaido pound net
	08 Apr.	121.0	29.8	2.0	Im	85.03	Usujiri, Hokkaido pound net
	14 Apr.	152.0	45.5	—	Mt	85.13	Usujiri, Hokkaido pound net[1]
	30 Apr.	134.0	35.0	—	—	85.25	Usujiri, Hokkaido pound net[2,3]
	05 May	132.0	36.7	2.0	Im	85.06	Usujiri, Hokkaido pound net
1986	03 Mar.	141.0	50.0	—		86.04	Otaru, Hokkaido gill net
	03 Mar.	146.0	45.0	—	Mt	86.07	Otaru, Hokkaido gill net
	03 Mar.	185.0	73.0	—	Preg.	86.06	Otaru, Hokkaido gill net
	10 Apr.	133.0	31.0	—	Im	86.09	Usujiri, Hokkaido pound net[2]
	14 Apr.	126.0	—	—	Im	86.11	Usujiri, Hokkaido pound net[2]
	14 Apr.	134.0	33.5	—	—	86.12	Usujiri, Hokkaido pound net[2,4]
	24 Apr.	162.0	69.1	8	Preg.	86.02	Usujiri, Hokkaido pound net
	24 Apr.	173.0	69.9	9.0	Preg.	86.03	Usujiri, Hokkaido pound net

Table 3 (Continued)

Year	Date	Body length (cm)	Body weight (kg)	Age (yr)	Reprod. cond.	Collection no.	Locality, comments
1986	24 Apr.	62.0	5.2	0	Fetus	86.03a	Usujiri, Hokkaido mother (86.03) in pound net
	03 May	166.0	86.0	8.5	Preg.	M27024	42°37'N 44°28'E
Unknown		92.4	16.0	0	Im	M27391	Nemuro, Hokkaido
Unknown		137.5	41.0	4.0	—	M27393	Nemuro, Hokkaido

[1]Live to Asamushi Aquarium, Aomori.
[2]Live to Otaru Aquarium, Otaru.
[3]Died later in captivity.
[4]Transferred from Otaru Aquarium to Tokyo.

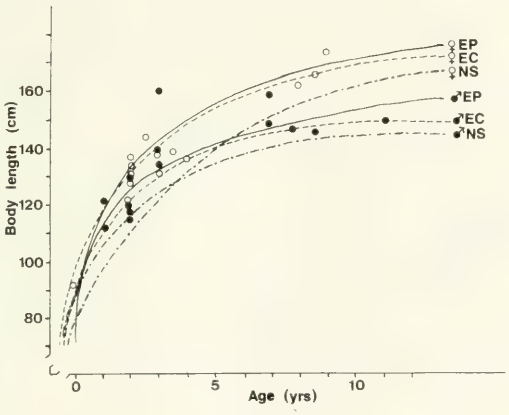

Figure 2

Age-length records for harbor porpoises in Japanese waters determined by Miyazaki et al. (1987) and the authors. Plotted against average growth curves for male and female harbor porpoises from the eastern North Pacific by Stuart and Morejohn (1980) (solid lines), eastern Canada by Gaskin and Blair (1977) (broken lines) and the North Sea by Van Utrecht (1978) (broken and dotted lines). Solid circles indicate male and open circles female porpoises from Japan.

Atlantic pattern of births in late spring or early summer and to mating between early and late summer. These populations are distributed in the same latitudinal zone and hence the same photoperiod regime. Sea surface temperature regimes are also similar, eg., Winn[6] and the Japan Meterological Agency (1986).

Harbor porpoises have testes that are large in proportion to body size (Fisher and Harrison, 1970; Gaskin et al., 1984). Miyazaki et al. (1987), comparing their material to data of Fisher and Harrison (1970), noted that adult harbor porpoises from Japanese waters had smaller testes than those from the North Atlantic and had weight ranges that did not overlap. They concluded that the difference in sampling periods in the two areas was not a factor (April–May off Japan v. May–September in the eastern North Atlantic, respectively). However, Gaskin et al. (1984) demonstrated a seasonal cycle of spermatogenesis, including a dramatic change in testis volume/size in adult harbor porpoises during June–August in the Bay of Fundy region. Read (1990a) concluded that the active mating period extended only from late June into July or occasionally early August. The specimens examined by Miyazaki et al. (1987) in April–May appear to have been collected before adult males had begun to exhibit seasonal spermatogenesis and testis enlargement.

P. phocoena appear to be a relatively asocial odontocete which has also undergone selection for sperm competition and for consequent development of proportionately large testes like some other cetaceans (Brownell and Ralls, 1986). In

[6]Winn, H. E. 1982. A characterization of marine mammals and turtles in the Mid- and North Atlantic areas of the U.S. outer continental shelf. U.S. Dep. Interior, Bureau of Land Management, Washington D.C., Final Rep. of the Cetacean and Turtle Assessment Program, 437 p.

the case of small marine mammals there is energetic advantage in evolving a limited mating period, together with a reduction in testis size out of the breeding season (Gaskin et al., 1984). Field observations of *Phocoena phocoena* populations suggest that there is little coherent school structure (eg., Amundin and Amundin, 1971; Watson, 1975; Watts and Gaskin, 1989); there is a mean group size of only two or three individuals, often mother, calf and yearling. Larger groups are generally temporary feeding aggregations. Similar results were obtained in studies of *Neophocoena phocoenoides* by Kasuya and Kureha (1979).

Distributional limits

The most southerly record of harbor porpoise from Japanese waters (Taiji, Wakayama, 34°15'N) quite closely parallels that for the oceanographically similar western North Atlantic (Cape Fear, southern N. Carolina) (Gaskin, 1984). The confirmed northernmost limit for the western North Pacific in recent years is represented by a number of sightings on the eastern side of the entrance of Shelikhova Bay, between 57°–58°N and 157°–159°E on 10–11 August 1989 (Miyashita and Doroshenko, 1990). On the eastern side of the North Pacific there are verified records in the Beaufort Sea as far as the MacKenzie Delta at about 70°N (Van Bree et al., 1977). Tomilin (1957), citing Sleptsov (unpublished data in manuscript report) who made observations in 1947–48, noted that the harbor porpoise was known in the USSR as far south as Peter the Great Bay, through the Sea of Okhotsk, around Kamchatka (where it was sometimes trapped in fishing nets), and northwards at least to Olyutorskii Bay at 60°N. A similar distribution was indicated by Klumov (1959). Tomilin (1957) thought its range might extend into the western part of the Chukchi Sea but gave no records. Sleptsov had also recorded porpoises in summer months around the Komandorski Islands and on both the east and west sides of the Kurile Islands. Miyashita and Berzin (1991) observed harbour porpoises just west of the southwestern Kuriles in early August 1990 and to the northwest of these islands and close to southeastern Sakhalin in mid-late August of the same year. Recent records from Alaska and the eastern Aleutian Islands are summarized by Gaskin (1984); and from the Attu island group in the western Aleutians, by Jones (1984).

Postulated seasonal changes in distribution in the N.W. Pacific

Given the similarities of life history parameters of harbor porpoise populations in both major oceans of the northern hemisphere, one way to estimate the likely range of the species in the western North Pacific and Bering Sea is to plot surface isotherms for values which generally appear to be limiting in regions where distribution is better known (Figs. 3 and 4). Winn[6], working off the eastern United States, found the species were confined almost entirely to coastal shelf waters and 90% of sightings were concentrated over water depths of 18–224 m off the east coast, in sea surface temperatures of 6.5–17.0°C. Barlow (1988) found that sightings off the west coast of the United States were most abundant over depths of 18–37 m and there were no sightings at depths greater than 110 m. Surface temperatures were not specified in this study. The areas of the North Pacific and Bering Sea which approximate these average conditions are shown for winter and summer in Figures 3 and 4. There is no doubt, however, that this species must sometimes follow productive convergence zones away from the coastal shelf, or it could not have attained its present distribution (Gaskin, 1992). Following the important offshore North Pacific record of Jones (1984) (see Introduction), Stenson and Reddin (1990) reported harbor porpoises over deep water in the Labrador Sea. Given the timing of seasonal occurrence in this region (Gaskin, 1984), these animals may have been travelling between the coastal shelves of Canada and West Greenland.

The surface temperature regime in the western North Atlantic indicated by Winn[6] more or less defines the productive, well-mixed boundary interaction zone between the cold, southward-flowing Labrador Current and its lesser branches and the warm northeastward-flowing North Atlantic Drift; but the temperature regime also defines the general range of the harbor porpoise. The range of the species in the northwestern Pacific, therefore, may be similarly defined by the interactions of the cold Oyashio water masses coming out of the western Bering Sea and Sea of Okhotsk with the northward and northeastward flow of the Kuroshio current and its subsidiaries around Japan (Hikosaka and Watanabe, 1957; Fukuoka, 1962). The Sea of Okhotsk is significantly colder in winter than the surrounding ocean regions, and the northern and western zones of it are characteristically ice-covered from late December to April, as is the Tartary Strait between Sakhalin Island and Siberia from early December to May (eg., Japan Meteorological Agency, 1986). While a small number of harbour porpoises either stay in or visit the western Bay of Fundy in winter (November–April) when water temperatures range from 1° to 4°C (Gaskin, 1984), any *P. phocoena* that stay around northern Japan during the winter months can be no further north in coastal waters than the extreme southeastern Sea of Okhotsk adjacent to the central and northern Kuriles and southwest of Sakhalin. The situation in most of the Sea of Okhotsk

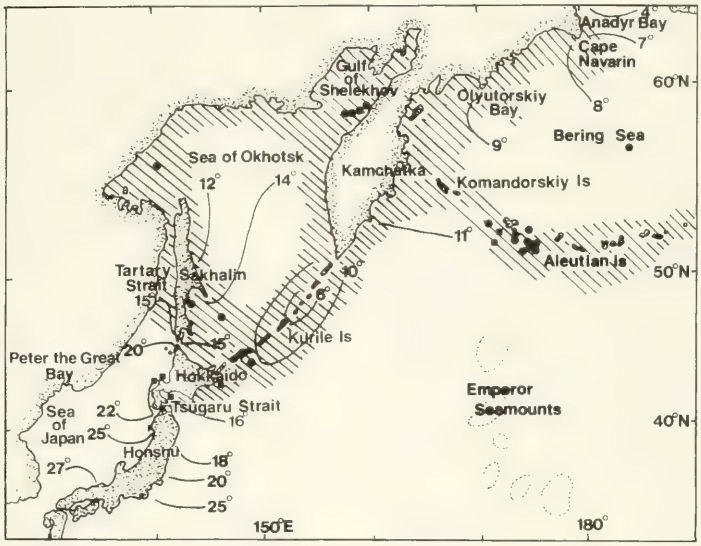

Figure 3

The western North Pacific and western Bering Sea, showing average summer surface isotherms (July–September) (Japanese Meteorological Agency 1986; Miyashita and Kasuya 1988; and Nasu 1963, 1966). Diagonal hatching indicates postulated summer range of about 90% of the harbor porpoise population based on criteria of Winn[6]. Solid circles indicate confirmed summer records. Solid squares are confirmed spring (April–June) records.

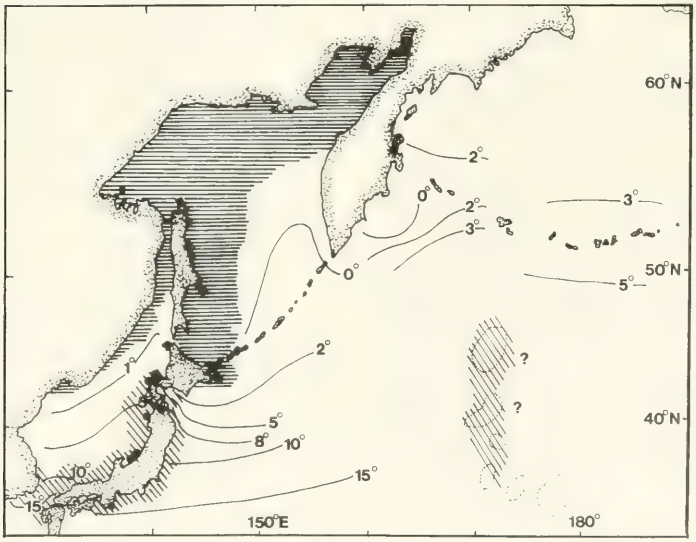

Figure 4

The western North Pacific and western Bering Sea, showing average winter surface isotherms (December–March) (Japanese Meteorological Agency 1986; Miyashita and Kasuya 1988; and Nasu 1963, 1966). Horizontal hatching indicates postulated winter range of about 90% of the harbor porpoise population based on criteria of Winn[6]. Solid circles indicate confirmed winter records.

must be analogous to that of the outer Estuary and inner Gulf of the St. Lawrence in eastern Canada (Laurin, 1976) and the Baltic Sea (Møhl-Hansen, 1954), where harbor porpoises leave ahead of the ice formation. The situation is likely to be different in the Sea of Japan, which in general has a much less severe marine climate than the Sea of Okhotsk (Hirano, 1957).

The records from Wakkanai show that harbor porpoises occur off northern Hokkaido during early winter in some years. In December 1986, a small zone of inshore surface water off Wakkanai was still at 9°C (Japan Meterological Agency, 1986). Some specimens have been taken incidentally by the gill-net fishery around the Shakotan Peninsula in January and February[7] where sea surface temperatures are about 4–5°C. The seasonal isotherm distributions suggest that in mid-winter *P. phocoena* might be expected to be found sometimes as far south as eastern Shikoku, to the southern tip of western Honshu and also along the east coast of the Korean peninsula (Fig. 3). Nevertheless, it has yet to be confirmed further south than Nishiyama (about 39°N) on the Japan Sea coast of Honshu (Institute of Cetacean Research, 1989). On the east coast of Honshu, the known southern limit of range at Taiji also coincides with the intrusion of deep water associated with the Fossa Magna geological discontinuity, which is a feature of the northern extremity of the Philippine tectonic plate margin (Pinet, 1992). The west coast manifestation of this structure occurs in Toyama Bay, at about 37°N.

In the summer months, harbor porpoises probably do not occur much further south on the west coast of Japan than the Tsugaru Strait and the western extremity of Hokkaido (Kawamura et al. 1983; Kawamura 1986) (Fig. 4), where surface temperatures of 12 to 16°C often persist through summer (Miyashita and Kasuya, 1988). The progression of seasonal reoccupation of northern waters in the western North Pacific is not well understood. The changes in distribution predicted here are based on the limits for the occurrence of about 90% of the population in the 6.5°–17.0°C range in the western North Atlantic (Winn[6]). Furthermore, Yurick (1977) noted that the greatest concentration of harbor porpoises in the lower Bay of Fundy was associated with the 8°–15°C surface isotherm zone.

Sea ice leaves the northern coast of Hokkaido usually in late April–early May and warmer surface waters of up to 8°C intrude into this region in May. By June surface temperatures of 5.0°–7.0°C occur as far north as the Komandorski Islands in average years, and by mid-July the same temperatures can be found off Cape Navarin at 63°N (Nasu, 1963, 1966). There is much year-to-year variation; in seasons with late development of summer conditions, the same regions can have surface temperatures as low as 2° to 4°C (Nasu, 1966). During August, surface waters reach 10°C both in this region and off Unalaska Island in the Aleutians (Nasu, 1966). Surface temperatures in the Sea of Okhotsk during June are often only 4°–5°C; but, by August–September 12°–15°C (Japan Meterological Agency, 1986). Although cooler intermediate water upwelling in summer around the central Kuriles is still only at 4°–6°C, highly productive boundary conditions for marine life are developed here (Hikosaka and Watanabe, 1957). The summer (August and early September) sightings of harbor porpoises in the Sea of Okhotsk during the extensive cruises of 1989 and 1990 (Miyashita and Doroshenko, 1990; Miyashita and Berzin, 1991) were almost all made over shelf regions; in contrast the pelagic central region was dominated by *Phocoenoides dalli*.

On the basis of distributional and energetic data from the western North Atlantic (Yasui and Gaskin, 1986), *P. phocoena* should tolerate a 6.5°–12°C surface regime with relative ease. Nevertheless, recent results of mitochondrial DNA comparisons of harbor porpoises in eastern Canadian waters (Wang et al., 1991) support the concept of distinct genetic demes coexisting within the regional range of the western North Atlantic population. We should not discount the possibility that some of these demes, either through differing dietary requirements or variation in thermoregulatory capacity, may be adapted to somewhat different surface temperature regimes. A specific area could be occupied by porpoises from one deme in summer and another in the winter, giving the appearance of continuous occupation by a single population. Migrations may exist but would be difficult to define without extensive tagging experiments.

In other areas of the northern hemisphere where the diet of harbor porpoises has been investigated (summarized by Gaskin, 1985), the main prey are schooling fishes of the coastal shelf, particularly herring *Clupea* sp., mackerel *Scomber* spp., squid, and small gadoids. Too little is known of the harbor porpoise in the western North Pacific to assess its dietary spectrum; in other areas, prey switches occur when herring availability is low (Recchia and Read, 1989). It seems, from the few data currently available, that harbor porpoises in Japanese waters eat sardines, anchovy, small hake, squid, and herring when encountered.

The intensity of inshore fishing activity in Japanese coastal waters is such that the harbor porpoise certainly has been subjected to some level of incidental catch historically, especially by set or drift nets of various kinds. Entrapments still occur; total annual incidental catches around the Shakotan Peninsula,

[7] Hiroshi Nitto, Otaru Aquarium, Otaru, Shakotan, Hokkaido, Japan, pers. commun.

Nemuro, and northwestern Honshu are possibly in the low hundreds[8]. Tobayama et al. (1991) noted that about 1,700 large trap nets and about 10 times that number of smaller-scale nets are in operation at some time of year in Japan. About 4,800 nets operate in Hokkaido waters; 2,500 on the Pacific coast of northern and western Honshu and perhaps about 1,500 on the northern half of the Sea of Japan coast of Honshu. All these regions are coincident with the distribution of the harbor porpoise in Japanese waters. Tobayama et al. concluded that where minke whale entrapments were concerned, the catches were largely unrecorded through the coastal fisheries statistics. Presumably this is also true of harbor porpoise entrapments. Given that we noted deaths of *P. phocoena* in gill nets not recorded in the annual statistics, there is significant under-reporting of incidental kills by gill netting too. We lacked the resources to conduct a survey to determine how large the incidental catch of harbor porpoises by fixed gear in Japanese waters might be.

The status of the harbor porpoise in Japanese waters is basically unknown. Anecdotal accounts from fishermen in the Usujiri region indicate that it is not particularly abundant in comparison to other dolphins (species not specified) and seasonal in occurrence (spring and fall). It is present in waters off Otaru in all but the months of July–September (Hiroshi Nitto, personal communication). A detailed assessment of its status in the western North Pacific is required. The species now appears to be threatened in some eastern and western North Atlantic waters (Gaskin, 1992). The limitations imposed by the fixed litter size of one, the relatively late age at first maturity and an annual reproductive cycle all point to little reproductive flexibility with which to respond to significant additional mortality from hunting or incidental capture (Woodley and Read, 1991; Gaskin, 1992).

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[9]Hiroshi Nitto, pers. commun.

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Use of a monogenean gill parasite and feasibility of condition indices for identifying new recruits to a seamount population of armorhead *Pseudopentaceros wheeleri* (Pentacerotidae)

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Abstract.—Recruitment of individuals from the epipelagic phase to the demersal armorhead *Pseudopentaceros wheeleri* population at Southeast (SE) Hancock Seamount has typically been recognized by the influx of fish with a high fatness index (FI; body depth relative to fork length). Reliance on this index was dictated by the peculiarity of the seamount life history stage in which armorhead cease somatic growth soon after recruitment to the seamount and FI declines during seamount residence until death. Limited sampling opportunities and variability in FI at the time of recruitment preclude the exclusive use of FI as a means of identifying newly arrived recruits among recruits-of-the-year and hence the timing of annual recruitment. Settlement and recruitment to the seamount population are synonymous. Efforts to develop a method of identifying new recruits were initiated by an examination of epipelagic and seamount (SE Hancock) armorhead for differences in macroparasites as well as hepatosomatic and visceral fat-somatic indices. Of the two condition indices, the hepatosomatic index held the most potential but was considered too labile because prerecruits probably experience decreases that vary according to energetic demands during seamount migration. The monogenean gill parasite *Microcotyle macropharynx* was highly prevalent among seamount individuals in all sampling periods but absent from epipelagics. Based on probable rapid infection and maturation, identification of new recruits was based on the absence of mature *M. macrophaynx*. Results indicate that significant new recruitment occurred only during the late spring to midsummer sampling periods, and the mean FI of new seamount recruits was lower than that of comparable size epipelagics.

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The armorhead *Pseudopentaceros wheeleri* (Hardy) in the North Pacific Ocean initially occupies an epipelagic and then demersal habitat during its life history. Progeny originate from winter spawning of the demersal armorhead population associated with the summit and upper slopes of the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts (Fig. 1) (Bilim et al., 1978; Borets, 1979). Larvae are initially found in surface waters around the seamounts (Fedosova and Komrakov, 1975; Borets, 1979) but soon move or are advected into subarctic waters of the central and northeastern Pacific (Boehlert and Sasaki, 1988). Here they feed in oceanic surface waters and undergo somatic growth, accumulate energy reserves, but experience no reproductive development. These epipelagic individuals appear deep-bodied and display a striking pattern of blue and silver blotches along their dorsal and lateral regions. The process and timing by which epipelagic individuals recruit back to the SE-NHR seamounts is not well understood (Boehlert and Sasaki, 1988). Individuals are primarily 28–33 cm fork length (FL) upon recruitment to the SE-NHR seamounts (Humphreys et al., 1989). Since recruits are similar in length and co-occur among the resident seamount population, settlement and recruitment to the seamounts are considered synonymous events (Humphreys et al., 1989). Unlike the epipelagics, the seamount population is demersal and virtually uniform in length, but morphologically variable. Three morphological variants (the "fat," "intermediate," and "lean" morphotypes) were previously recognized and found

to represent different stages of the demersal seamount phase (Humphreys et al., 1989). This variation intergrades from the deep-bodied, overall bluish-gray coloration of presumably recent recruits (fat morphotype) through progressively leaner forms of uniformly brownish coloration (intermediate and lean morphotypes). Relative body depth refers to the ratio of body depth at first anal spine to FL and hereafter is called the fatness index (FI; Somerton and Kikkawa, 1992). Usage of FI values recognizes that these variations form a continuum rather than discrete changes and has replaced classification by morphotype (Somerton and Kikkawa, 1992). Declining FI reflects the transformation by individuals as the elapsed time of seamount residence increases. During this phase, somatic growth ceases upon recruitment, and stored energy reserves are eventually mobilized for reproductive development and spawning. These processes contribute to the decline in FI and ultimately lead to death (Humphreys et al., 1989).

The discovery of large aggregations of armorhead over the summits and upper slopes of SE-NHR seamounts (Fig. 1) during exploratory work by the former Soviet Union in 1967–1969 (Komrakov, 1970) led to a full-scale bottom trawl fishery in this region by both Japanese and the former Soviet trawl fleet (Uchida and Tagami, 1984). By the end of 1975, the cumulative combined fleet catch of armorhead was some 880,000 metric tons (t). Total annual catch of armorhead by the Japanese trawl fleet declined dramatically after 1976 (Humphreys et al., 1984) and continues to remain low throughout the SE-NHR region (R. Humphreys, unpubl. data). In 1977 the Hancock Seamounts, located in the southermost portion of the SE-NHR trawl fishery, came under U.S. jurisdiction with the implementation of the 200-mile fishery conservation zone (Humphreys et al., 1984). During 1978–1984, several Japanese trawlers were allowed to fish the Hancock Seamounts but were regulated by permit and an annual catch quota (Uchida and Tagami, 1984;

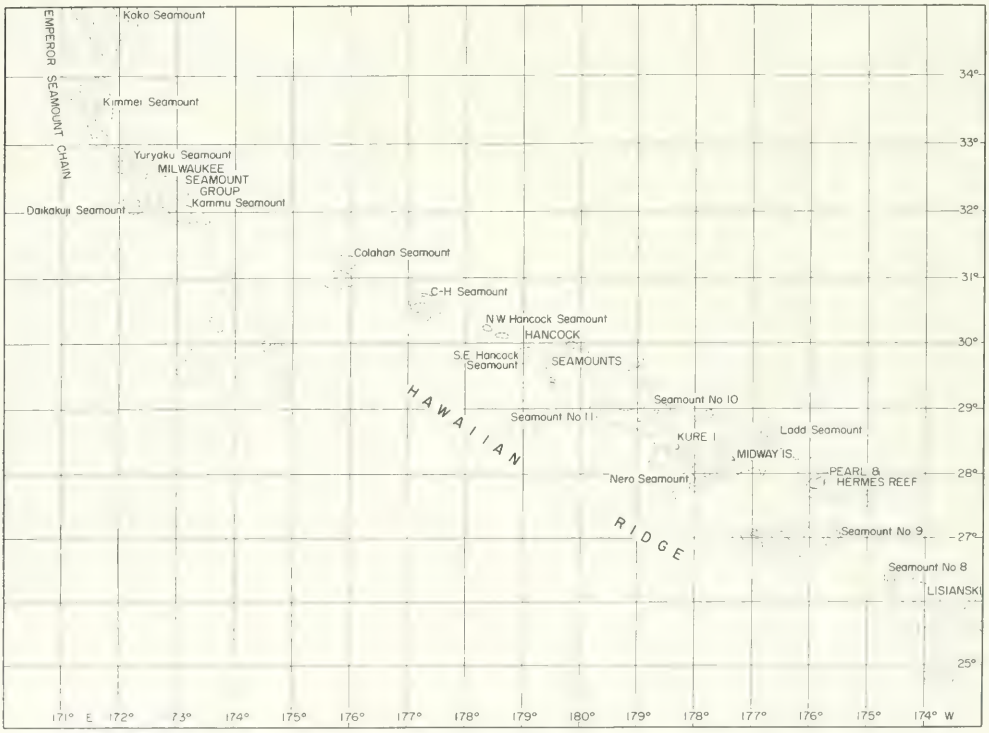

Figure 1

The major habitat of dermersal armorhead is located over the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts extending from Koko Seamount to the northwest down through the Hancock Seamounts in the southeast region.

Somerton and Kikkawa, 1992). Owing to sustained low annual catches at the Hancock Seamounts, the National Marine Fisheries Service (NMFS) Honolulu Laboratory implemented both a research stock assessment program in 1985 and recommended institution of a moratorium (in effect since 1986) prohibiting trawl fishing at the Hancock Seamounts (Somerton and Kikkawa, 1992). The remainder of the SE-NHR seamounts, which represent some 90% of the historical trawl fishery in terms of habitat and overall catch, lie in international waters and under no fishery management control. As increases in armorhead biomass at Hancock and other SE-NHR seamounts appear to depend exclusively on recruitment, recent work has focused on examining the temporal pattern of seamount recruitment and the biological characteristics of new recruits. Boehlert and Sasaki (1988) used monthly length-weight data recorded by the Japanese at four SE-NHR seamounts during May 1972–December 1973 to estimate the seasonality of recruitment. Assuming that new recruits have a condition factor of ≥2.0, they found recruitment highest during April–May 1973 and secondary peaks in August 1972 and July 1973. Annual recruitment to Southeast (SE) Hancock Seamount, one of two guyots composing the Hancock Seamounts, was sporadic between 1978 to 1990. Strong recruitment (≥50% of population biomass) at SE Hancock Seamount occurred only in 1980 and 1986, and moderate recruitment (ca. 20–30% of population biomass) in 1988 and 1990, based on catch per unit of effort (CPUE) and FI distributions derived from Japanese trawl data and NMFS stock assessment surveys (Somerton and Kikkawa, 1992).

Little further progress, however, has been made in discerning the timing of recruitment and biological characteristics of newly arrived recruits. The apparent temporal variability in recruitment, the change in FI during time elapsed between recruitment and sampling, coupled with limited sampling opportunities, make the identification and study of new recruits and their temporal recruitment pattern problematic. A potential alternative for identifying newly recruited armorhead uses biological indicators to distinguish a new seamount arrival from longer resident armorhead. Parasites have been frequently used as biological indicators in fish and their benefit to studies of fish stock separation, movement, and diet are numerous (Williams et al., 1992). In relation to seamount studies, differences in the trematode parasite fauna of sablefish off Canada's west coast led Kabata et al. (1988) to surmise that seamount populations of sablefish are distinct and separate from those sablefish inhabiting the continental slope. Since seamount armorhead populations are derived from epipelagic individuals, we examined specimens of both life history phases for parasite differences and other distinguishing features. We report on the feasibility of using a monogenean gill parasite and two condition indices as potential indicators of new seamount recruits.

Methods

Epipelagic specimens of *P. wheeleri* (n = 53) were incidentally captured from the central North Pacific (around lat. 45°N, long. 155°W) in July 1984 and 1985 and from the eastern North Pacific (around lat. 46°N, long. 129°W) in July 1985 by the Japanese fishing vessels *Oshoro Maru* and *Tomi Maru No. 88*, respectively, during salmon longline and surface drift gillnet operations. These specimens were saved intact and stored frozen prior to examination. Specimens of seamount armorhead (n = 1,220) were collected from the southern end of the SE-NHR at SE Hancock Seamount (29°48'N, 179°04'E; see Fig. 1) by bottom longline gear during research cruises of the NOAA ship *Townsend Cromwell* in June 1985, August and October 1986, April and August 1987, and January, July, August, and November 1988. All seamount specimens were derived from efforts beginning in 1985 to estimate armorhead relative abundance (catch per unit of effort) at SE Hancock Seamount by using standardized assessment techniques described in Somerton and Kikkawa (1992). Seamount specimens were either saved intact and stored frozen, or gills and viscera were removed and preserved at sea in either alcohol-formalin-acetic acid (AFA) solution or placed in a dilute (0.0004%) formalin solution for several hours and then preserved in 10% formalin. Collection data for armorhead specimens included body weight, FL, body depth at first anal spine, sex, and date and location of capture. Measurements were made to the nearest millimeter, and body weight to nearest gram.

Under a dissecting microscope, the gill arches and visceral organs of armorhead specimens were examined for macroparasites. Guidelines proposed by Sindermann (1983) were followed to determine which species have potential as biological tags. Ideal parasite characteristics include ease of detection and identification, a single host-life cycle, and temporal stability in prevalence. Furthermore, the parasite should persist in the host during the study, and prevalence should differ significantly between study areas. These criteria were best fulfilled by the monogenean *Microcotyle macropharynx* (Mamaev), based on examinations of the seven parasite taxa (monogenean *Trochopus* sp., digenean *Bivesicula* sp., larvae of the nematode *Anisakis* type I, nematode *Hysterothylacium*

sp., an unidentified caligoid copepod, and juveniles of an unidentified gnathiid isopod) found in the epipelagic and seamount armorhead collected in June 1985 and August 1986. Subsequent examinations of armorhead were restricted to the gills where *M. macropharynx* were exclusively found. Specimens of *M. macropharynx* were readily distinguished from *Trochopus* sp. by the disk-shaped opisthaptor of the latter monogenean. All specimens of *M. macropharynx* were initially identified as that of *M. sebastis* though the pharynx of these specimens appeared to be unusually large[1]. During the review process, a new species description (Mamaev, 1989) of the monogenean *M. macropharynx* collected in 1969–70 from *P. richardsoni* (=*P. wheeleri*) in the Hawaiian Islands region was brought to the attention of the senior author. Subsequently specimens initially identified as *M. sebastis* were re-examined and all found to be *M. macropharynx*[2]. The large pharynx (in relation to the anterior suckers) of *M. macropharynx* distinguishes this species from all other species of *Micocotyle* (Mamaev, 1989). Each *M. macropharynx* was staged as either immature or potentially mature, based on absence or development of the paired yolk ducts, respectively. These organs are the last to develop before egg development in the related species *M. sebastis* (Thoney, 1986). All parasite taxa were saved and stored in 70% ethyl alcohol. Prevalence and mean intensity of *M. macropharynx* in seamount armorhead were computed for each sampling period. Following the terminology defined in Margolis et al. (1982), prevalence (expressed as a percentage) refers to the number of host species infected with a particular parasite species, divided by the number of hosts examined; and mean intensity is derived by dividing the total number of a particular parasite species by the number of individual hosts infected by that parasite. Prevalence and mean intensity data from seamount armorhead were partitioned into two FI groups of <0.26 and ≥0.26. This grouping is based on the observation that 0.26 was the lowest FI found for epipelagic armorhead in this study and thus a possible minimum FI for newly arrived seamount recruits.

Liver and visceral fat weights were also determined for the 27 epipelagic armorhead >27.5 cm FL (of comparable length to seamount individuals) and 410 seamount armorhead collected during October 1986 (n = 115) and January (n = 195), July (n = 18), and November 1988 (n = 82). Liver and visceral fat deposits were removed from the body cavity, blotted dry, and weighed to the nearest 0.1 g. Liver and visceral fat weights are expressed in relation to total body weight and referred to as the hepatosomatic index (HSI) and visceral fat-somatic index (VFSI), respectively. Data was arcsine transformed and tested for normality with the Lilliefor's method of the Kolmogorov-Smirnov test (Wilkinson, 1990). Sample means were compared by either t-test, or by Mann-Whitney test if samples remained non-normal (Wilkinson, 1990).

Estimates of the proportion of recruits-of-the-year to the total SE Hancock armorhead population during each sampling period were based on stock-assesssment-derived FI distributions of the armorhead population. That proportion of the FI distribution ≥0.26 were considered recruits-of-the-year. Data and procedures used to calculate the population FI distribution are presented in Somerton and Kikkawa (1992). The proportion of recruit-of-the-year armorhead in each sampling period un-infected by mature stages of *M. macropharynx* was estimated from results of the prevalence data for those armorhead (from samples examined for *M. macropharynx*) with a FI ≥0.26.

Results

Microcotyle macropharynx were not present in any of the 53 epipelagic armorhead examined but were present in all 775 seamount armorhead with FI <0.26 and in 417 (93.7%) of 445 specimens with FI ≥0.26. Among seamount armorhead with FI <0.26, both the combined (irrespective of maturity stage) category and the immature and mature stage of *M. macropharynx* were highly prevalent (>75%) in all nine sample periods surveyed (Table 1). A similar pattern of high *M. macropharynx* prevalence was found among the seamount armorhead with FI ≥0.26 although instances of lower prevalence appear during the two earliest sample periods (Table 1). Mean intensity of immature *M. macropharynx* in both FI groups was considerably lower in each sample period than the corresponding mean intensities of the mature stage and combined category (Table 2). Mean intensity of mature stage *M. macropharynx* in each sample period and FI group was sufficiently high to ensure easy detection in armorhead infected with mature stage individuals of this monogenean. A wide range in sizes of *M. macropharynx*, including mature stages with eggs, was present among the gills of armorhead, indicating that this parasite has a monoxenous life cycle.

Seamount armorhead without mature *M. macropharynx* represented 5.2% (64) of the 1,220 fish examined. Among those seamount armorhead found un-

R. R. Payne, Department of Biological Sciences, Biola Univ., La Mirada, CA, personal commun. 1988.

[2]R. R. Payne, Department of Biological Sciences, Biola University, La Mirada, CA, pers. commun. 1992.

Table 1

Prevalence of the monogenean *Microcotyle macropharynx* in the gills of armorhead *Pseudopentaceros wheeleri* by fatness index (FI) groups of <0.26 and ≥0.26, collected from Southeast Hancock Seamount during 1985–88. Within each FI group, prevalence is further categorized by maturity stage of monogenean or regardless of (combined). Prevalence expressed as a percentage of total number (*n*) of armorhead examined. Differences in (*n*) between maturity stages indicates missing data. Occurrences of combined (*n*) exceeding (n) of both maturity stages represents instances where monogeneans from an additional sample were not staged.

	FI <0.26			FI ≥0.26		
Sample period	Immature stage	Mature stage	Combined	Immature stage	Mature stage	Combined
Jun 1985	98.0	95.9	100.0	70.0	45.0	80.0
	n=49	*n*=49	*n*=50	*n*=20	*n*=20	*n*=20
Aug 1986	93.0	100.0	100.0	68.8	66.7	75.0
	n=57	*n*=57	*n*=58	*n*=48	*n*=48	*n*=48
Oct 1986	92.5	100.0	100.0	84.9	96.2	99.1
	n=80	*n*=80	*n*=80	*n*=106	*n*=106	*n*=107
Apr 1987	80.6	100.0	100.0	85.2	96.3	96.3
	n=134	*n*=137	*n*=137	*n*=27	*n*=27	*n*=27
Aug 1987	88.2	100.0	100.0	95.8	89.6	95.8
	n=68	*n*=68	*n*=68	*n*=48	*n*=48	*n*=48
Jan 1988	94.5	100.0	100.0	100.0	100.0	100.0
	n=181	*n*=183	*n*=183	*n*=12	*n*=12	*n*=12
Jul 1988	93.3	100.0	100.0	78.8	80.8	90.4
	n=45	*n*=45	*n*=45	*n*=52	*n*=52	*n*=52
Aug 1988	93.6	100.0	100.0	90.4	78.8	94.2
	n=47	*n*=47	*n*=47	*n*=52	*n*=52	*n*=52
Oct–Nov 1988	96.6	97.7	100.0	98.7	97.5	100.0
	n=87	*n*=87	*n*=87	*n*=79	*n*=79	*n*=79

Table 2

Mean intensity of the monogenean *Microcotyle macropharynx* in the gills of armorhead *Pseudopentaceros wheeleri* by fatness index (FI) groups of <0.26 and ≥0.26, collected from Southeast Hancock Seamount during 1985–88. Within each FI group, mean intensity is further categorized by maturity stage of monogenean or regardless of (combined). Sample size from which mean intensity is based on is denoted by (*n*). Differences in (n) between maturity stages indicates missing data. Occurrences of combined (*n*) exceeding (n) of both maturity stages represents instances where monogenean was present but stage of maturity not determined. Smaller sizes of (n) in this table compared to the (*n*) of corresponding cells in Table 1 indicates instances where data on prevalence, but not mean intensity, is available.

	FI <0.26			FI ≥0.26		
Sample period	Immature stage	Mature stage	Combined	Immature stage	Mature stage	Combined
June 1985	12.23	35.72	52.06	4.64	95.22	57.63
	n=48	*n*=47	*n*=50	*n*=14	*n*=9	*n*=16
Aug 1986	9.09	63.84	72.12	6.91	30.41	34.03
	n=53	*n*=57	*n*=58	*n*=33	*n*=32	*n*=36
Oct 1986	9.74	88.01	97.03	5.42	65.77	68.18
	n=74	*n*=80	*n*=80	*n*=90	*n*=102	*n*=106
Apr 1987	16.21	65.17	79.92	19.23	162.86	181.14
	n=79	*n*=24	*n*=24	*n*=13	*n*=14	*n*=14
Aug 1987	17.97	58.48	75.48	14.42	58.21	72.68
	n=31	*n*=33	*n*=33	*n*=19	*n*=19	*n*=19
Jan 1988	15.84	56.66	71.11	20.44	110.00	130.44
	n=31	*n*=35	*n*=35	*n*=9	*n*=9	*n*=9
Jul 1988	14.47	27.69	41.25	7.67	36.47	37.80
	n=30	*n*=32	*n*=32	*n*=18	*n*=17	*n*=20

infected by mature stage *M. macropharynx*, virtually all were of a FI ≥0.26 (Table 3). The four armorhead with FI <0.26 and uninfected by mature *M. macropharynx* had FI values disjunct from similarly un-infected armorhead with FI ≥0.26 (Fig. 2). Mean FI's of the seamount armorhead group (FI ≥0.26) without mature *M. macropharynx* (x = 0.291) and the epipelagic group (x = 0.307) were significantly different (t-test, $P < 0.001$). From samples of seamount armorhead (FI ≥0.26) examined for prevalence of mature stage *M. macropharynx*, the percentage of those found without mature *M. macropharynx* was higher in the June–August samples (Table 3). However, these latter results did not always correspond with peaks in the proportion of the seamount armorhead population (with FI ≥0.26) obtained from stock assess-

Table 3

Percent absence of mature stages of the monogenean *Microcotyle macropharynx* from the gills of armorhead *Pseudopentaceros wheeleri* by fatness index (FI) groups of <0.26 and ≥0.26, sampled from Southeast Hancock Seamount during 1985–88. Sample size examined for each category denoted by (*n*).

Sample period	FI <0.26	FI ≥0.26
Jun 1985	4.1	55.0
	n=49	*n*=20
Aug 1986	0	33.3
	n=57	*n*=48
Oct 1986	0	3.8
	n=80	*n*=106
Apr 1987	0	3.7
	n=137	*n*=27
Aug 1987	0	10.4
	n=68	*n*=48
Jan 1988	0	0
	n=183	*n*=12
Jul 1988	0	19.2
	n=45	*n*=52
Aug 1988	0	21.2
	n=47	*n*=52
Nov 1988	2.3	2.5
	n=87	*n*=79

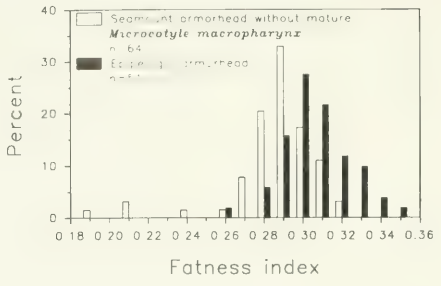

Figure 2

Distribution of fatness index for specimens of epipelagic and Southeast Hancock Seamount armorhead *Pseudopentaceros wheeleri* without mature parasites of *Microcotyle macropharynx*.

ment surveys (Fig. 3; data taken Somerton and Kikkawa (1992) from FI distributions for each sample period except November 1988).

Mean HSI (x = 3.147; Fig. 4) of the epipelagic group was significantly different from that of seamount armorhead with FI ≥0.26 (x = 1.358, Mann-Whitney test, $P < 0.001$) and those with FI <0.26 (x = 1.028, t-test, $P < 0.001$). Furthermore, none of the seamount armorhead except for two individuals in the FI ≥0.26 group had HSI values exceeding the lowest value (2.154) of the epipelagic group. Differences between the mean HSI of the two seamount FI groups were

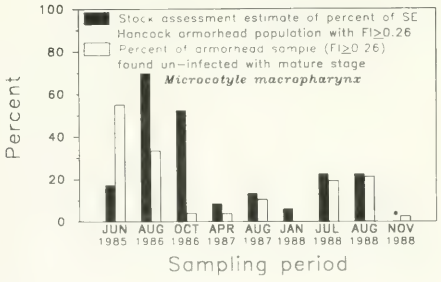

Figure 3

Percent of armorhead *Pseudopentaceros wheeleri* samples (fatness index (FI) ≥0.26) without mature *Microcotyle macropharynx* (from Table 3), and the percent of SE Hancock armorhead population with FI ≥0.26; the latter estimated from stock assessment surveys during each of the periods (except November 1988) where armorhead were sampled for *M. macropharynx* infection.

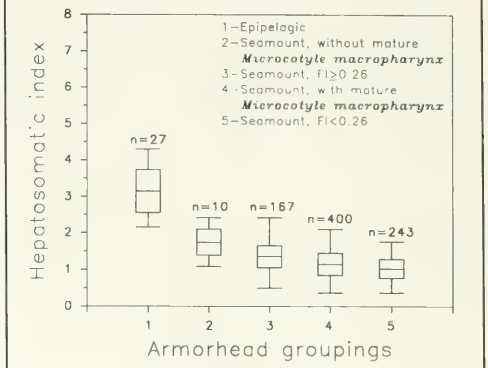

Figure 4

Hepatosomatic index by each grouping of armorhead *Pseudopentaceros wheeleri*. The mean is indicated by the mid-point horizontal line within each box, one standard deviation about each mean is denoted by the box, and the range is displayed as the horizontal lines above and below the box.

also highly significant (Mann-Whitney test, $P < 0.001$). Regardless of FI value, the difference in mean HSI between epipelagics and seamount armorhead without (x = 1.744, t-test, $P < 0.001$) and with (x = 1.148, t-test, $P < 0.001$) mature *M. macropharynx* remained significantly different, as were differences between the latter two groups (t-test, $P < 0.001$). The seamount armorhead group without mature *M. macropharynx* exhibited the least overlap in HSI values with other seamount groups (Fig. 4).

For the epipelagic group, mean VFSI (x = 2.152; Fig. 5) was significantly different from seamount armorhead with FI ≥0.26 (x = 3.580, t-test, $P < 0.001$) and those with FI <0.26 (x = 2.933, Mann-Whitney test, $P = 0.007$). Mean VFSI differences between the latter two seamount groups were also significant (Mann-Whitney test, $P < 0.001$). The mean VFSI of the epipelagic group was also significantly different from that of seamount armorhead with (x = 3.185, Mann-Whitney test, $P < 0.001$) and without (x = 3.663, t-test, $P = 0.009$) mature *M. macropharynx*, whereas the latter two seamount groups did not significantly differ in mean VFSI (Mann-Whitney, $P = 0.364$). Overlap in VFSI among the various groups (Fig. 5) was substantially greater than exhibited for HSI.

Discussion

The complete absence of the monogenean *M. macropharynx* from all epipelagic armorhead exam-

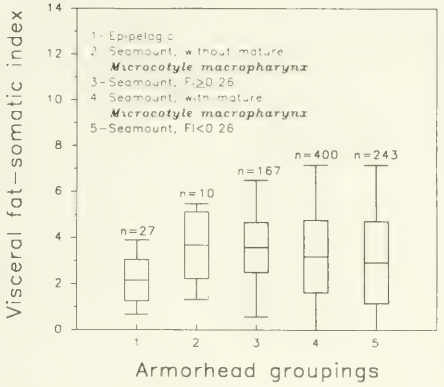

Figure 5

Visceral fat-somatic index by each grouping of armorhead *Pseudopentaceros wheeleri*. The mean is indicated by the midpoint horizontal line within each box, one standard deviation about each mean is denoted by the box, and the range is displayed as the horizontal lines above and below the box.

ined, and its high prevalence among seamount armorhead during all sample periods, support the notion that infestation of this parasite originates at the seamount. The prevalence of immature *M. macropharynx*, particularly for those armorhead with FI <0.26, indicates that infestation at the seamount is probably a continuing process. The presence of *M. macropharynx* in all 775 seamount armorhead with FI of <0.26 also negates the likelihood of a sizable proportion of seamount armorhead becoming uninfested over time.

The maturation rate of *M. macropharynx* on armorhead remains undetermined, but Thoney (1986) has found the oncomiracidia of the morphologically similar *M. sebastis* capable of maturing within 12 days on the gills of black rockfish *Sebastes melanops* (Girard) off northern California. Although armorhead are different hosts, inhabit greater depths, and are geographically distant from black rockfish, the temperature range (12°–17°C) used by Thoney (1986) to determine the maturation time of *M. sebastis* is similar to that found on the summit and upper slope of SE Hancock Seamount. Assuming this rapid maturation also occurs among *M. macropharynx* infecting armorhead, we propose that armorhead with exclusively immature *M. macropharyx* have probably only recently become infested and have seamount residence times that differ little from those of uninfested armorhead. The 0.26 FI value may represent a lower FI limit for potential new recruits, for only 6% of seamount armorhead without mature *M. macropharynx* had FI values <0.26 and the lowest FI value of the epipelagics examined was 0.26. However, an unknown proportion of armorhead with FI ≥0.26 perhaps recruit during the previous year at sufficiently high FI values that these FI values still remain above 0.26 when sampled the following year. Even in this situation, such individuals would be infected with mature *M. macropharynx* by the time they are sampled the following year and therefore not mistaken for new recruits. The presence of *M. macropharynx* probably cannot identify recruits that arrived one or several months before sampling if initial infection occurs soon after recruitment and *M. macropharynx* mature some two weeks thereafter. Hence, our technique can detect only new recruits among the recruit-of-the-year population and is therefore limited to determining whether recruitment is a continuous process.

Of the two condition indices, VFSI shows little promise as an indicator of new recruits, for the VFSI values in epipelagic and seamount individuals broadly overlap, regardless of FI and the presence or absence of mature *M. macropharynx*. Conversely, virtually no overlap in HSI values occurs between epipelagic individuals and any of the seamount armorhead groupings. Preliminary results of sagittal otolith increment enumeration on epipelagic individuals (>27.5 cm FL) and SE Hancock armorhead without mature *M. macropharynx* indicates a common age around 2.5 years (R. Humphreys, unpubl. data). This appears to suggest that those epipelagic individuals examined either remain pelagic or represent "strays" who will eventually or have begun a delayed movement that will result in recruitment to a SE-NHR seamount but a protracted epipelagic phase. The higher mean HSI value of these epipelagics versus seamount armorhead (FI ≥0.26) un-infected by mature *M. macropharynx* suggests that HSI decreases somewhere during the period between movement to the seamounts and time of capture after seamount recruitment. To explain the higher mean HSI of epipelagics and evaluate its efficacy as a recruitment indicator, this forementioned period must be examined in relation to both time and distance.

Of the 27 epipelagic individuals with FLs comparable to seamount populations (>27.5 cm FL) and least distant from the SE-NHR seamounts, 22 were collected around lat. 45°N, long. 155°W; some 2,860 km northeast of the SE-NHR seamounts. Summertime captures of smaller (22–26 cm FL) epipelagics are also frequent from the above general location and indicate an age of some 1.5 years (Boehlert and Sasaki, 1988; R. Humphreys, unpubl. data). Since recruit-of-the-year seamount armorhead are age 2.5 years (R. Humphreys, unpubl. data), these smaller individuals apparently represent the year class which recruit to the SE-NHR

seamounts in the following year. Allowing a one-year period (recruitment by the following summer) for individuals of the 1+ epipelagic year-class to move from the open ocean site (45°N 155°W) to the SE-NHR seamounts and also that the total distance traversed is twice the straight-line distance between these sites (assuming this is comparable to results of open-sea tracking of coho salmon *Oncorhynchus kisutch* reported in Ogura and Ishida (1992)), a rough estimate of the average ground speed required is 18 cm/s if currents are disregarded. Based on a length (27.1 cm FL) midway between the average FL of 1+ (x = 24.49 cm FL) and 2+ year-old (x = 29.64 cm FL) epipelagic specimens collected during summers at the open ocean site, individuals would need to swim 0.66 body length/s to arrive at an SE-NHR seamount one year later. This speed is close to the mean sustained cruising speeds (0.2–0.5 body length/second) typical of horizontally migrating fish (Beamish, 1978). Since no evidence exists of gonadal maturation in the epipelagic stage (Humphreys et al., 1989), the major energy demand during seamount migration is likely locomotion, in addition to basal metabolism. It is unknown whether feeding occurs during this migration; however, McKeown (1984) suggests that even if fish species feed during migration, the added energy intake may be negated by the additional energy required for feeding activity. Regardless of feeding, lipid reserves are typically used during migration (McKeown, 1984), and their storage in the liver and muscle makes these prime sites from which energy reserves can be drawn (Woodhead, 1975). As such, the liver is susceptible to net decreases in weight by the end of migration; an example of this occurs among migrating Barents Sea cod *Gadus morhua* (Woodhead, 1975). Evidence of fewer prey contents among higher FI armorhead examined at SE Hancock[3] indicates that recent recruits initially may feed little at the seamounts. This suggests that the liver remains susceptible to continued energy depletion and therefore continued decrease in liver weight. Assuming that liver weight is declining relatively faster than body weight, the HSI will not only decrease by the time of initial recruitment to the seamount but perhaps also during the interval between initial recruitment and sampling. Therefore, an annual or seasonal change in mean HSI among new recruits may be caused by inter- or intra-annual differences experienced by epipelagics in terms of environmental conditions and distance traversed during the seamount migration, along with an unknown time gap between initial recruitment and sampling. Hence, using HSI as a recruitment indicator appears to be inherently more labile and thereby less feasible and reliable than the method based on the absence of mature *M. macropharynx*.

The parasite approach revealed that new recruitment coincided primarily with the late spring and midsummer sampling periods. Somerton and Kikkawa (1992) have analyzed the recruitment patterns of armorhead to SE Hancock, using the modal progression of FI in which separate modes are considered annual cohorts. If a modal influx of high FI fish represents a "recruitment cohort," estimated recruitment was highest in terms of biomass (58 t) and percentage (79%) of the SE Hancock population during August and October 1986, whereas the next highest recruitment (8 t and 21% of the population, respectively) in July and August 1988 was comparatively modest. Interestingly, however, the level of new recruitment, as determined by the percentage of sampled armorhead (FI ≥0.26) un-infected with mature *M. macropharynx*, was highest in June 1985 and very low in October 1986. These results appear contrary to stock assessment based estimates of modest and high proportions of recruit-of-the-year armorhead (FI ≥0.26) in the seamount population during June 1985 and October 1986, respectively (see Fig. 2). These results can be reconciled if we consider that the rate of post-recruitment decline in FI (estimated at 0.00169/month; Somerton and Kikkawa (1992)) does not allow one to decipher between recruits which may have just arrived and those which arrived months prior to sampling. The absence of mature stage *M. macropharynx* appears to be the only criteria examined in this study capable of detecting whether a recruit-of-the-year (FI ≥0.26) is a new arrival to the seamount. Based on this criteria, the level of new recruitment during the months sampled was highest in June, less so in July and August, and very low during October, November, January, and April. These results tend to corroborate evidence of similar seasonal armorhead recruitment at other SE-NHR seamounts (Boehlert and Sasaki, 1988).

Recruits identified via the parasite approach typically have FI values ≥0.26 (x = 0.291). However, a high FI value alone provides no assurance that an individual is a new recruit. The difference in mean FI between epipelagic individuals and new recruits (uninfected with mature *M. macropharynx*) may indicate that FI decreases sometime before epipelagics of recruitment size reach the seamounts. This can be adequately examined only after both groups are further sampled.

Acknowledgments

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[3]M. P. Seki, NMFS Honolulu Laboratory, pers. commun. January 1992.

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Variability of zooplankton biomass and dominant species abundance on Georges Bank, 1977–1986

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Abstract.–Annual and seasonal variability of Georges Bank zooplankton biomass and dominant species abundance are described and related to variations in mean surface temperature and average depth distribution. Data were obtained from plankton samples collected bimonthly with a 0.333-mm mesh net throughout a ten-year period: 1977–86. Biomass was measured by displacement volume and the dominant species analyzed were the copepods *Calanus finmarchicus, Pseudocalanus minutus, Centropages typicus, Centropages hamatus,* and *Metridia lucens.*

Biomass levels were high in 1977 through 1979, low in 1982 through 1984. Biomass and copepod abundance in the spring of 1977 were extraordinary. Measurements over the entire bank were two to three times above a ten-year median. Unlike the first five years of monitoring, the average seasonal biomass cycle was not coherent from 1982 through 1986. Departures from the average seasonal cycle occurred several times during the second half of the time series.

Calanus finmarchicus and *Pseudocalanus minutus* abundance trends were nearly identical, suggesting that their populations may be affected by similar factors. *Centropages hamatus* abundance in the central shoal depth zone (<61 m) was related to surface temperature variability and its spring abundance estimates were indirectly proportional to the abundance of other dominant copepods. *Centropages typicus* counts in autumn 1985 were nearly double all other years, and *Metridia lucens* abundance surged in late spring 1979 but was low from 1983 through 1986.

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Fishery Bulletin 91:464–474 (1993).

Zooplankton biomass has long been recognized as an important index for estimating the seasonal and annual variability of secondary production in marine ecosystems. Zooplankton play a key role in pelagic food chains, serving as the connecting link between primary producers and secondary consumers. The availability of zooplankton as food for larval fish is thought to be one of the key factors determining year class strength of commercial fish species (Cushing, 1978).

The rich fishing grounds of Georges Bank in the northwest Atlantic have been the focus of zooplankton studies since the turn of the century. The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program (Sherman, 1980) has monitored the U.S. Northeastern continental shelf marine ecosystem from 1977 through 1987 with bimonthly surveys, measuring a variety of biological and physical parameters. During the first five years of MARMAP monitoring, zooplankton biomass on Georges Bank formed a coherent seasonal pattern, not changing significantly from year to year (Sherman et al., 1983). Comparison of this data to that collected by Bigelow (1926) from 1912 to 1920 showed that biomass levels, species composition, and abundance estimates of dominant species were essentially the same in both studies. Sherman et al. (1987) described in greater detail the seasonal cycle of Georges Bank zooplankton and how it relates to ichthyoplankton life histories. Additional studies (Davis, 1984; Meise-Munns et al., 1990) of Georges Bank zooplankton have used subsets of this large data base to help define and simulate seasonal cycles of dominant species in relation to environmental parameters.

The purpose of this paper is to further describe the Georges Bank zooplankton community by utilizing data collected during MARMAP surveys from 1977 to 1986. The annual and seasonal variability of zooplankton biomass captured with 0.333-mm mesh nets is reported and related to changes in the abundance of the five dominant zooplankton species (Sherman et al., 1987). The average depth distribution of biomass and dominant species abundance is described and departures from it are compared to overall population variability.

The sensitivity of the above parameters to surface water temperature readings is also examined to consider the potential effects of climatic change on Georges Bank zooplankton populations. This study is part of a continuing long-term investigation by the National Marine Fisheries Service (NMFS), which monitors the zooplankton component of the U.S. Northeast shelf ecosystem.

Methods

Plankton samples were collected at monthly to bi-monthly intervals at 32 station locations during MARMAP surveys on Georges Bank (Fig. 1).

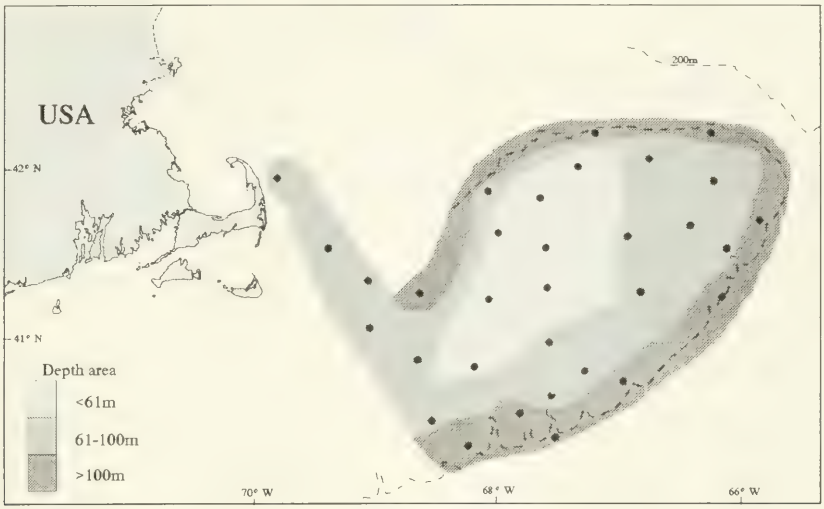

Figure 1

Location of standard MARMAP (Marine Resources Monitoring, Assessment, and Prediction program) stations on Georges Bank off the U.S. Northeast coast, 1977–86.

Plankton samples were also collected on trawl and dredge surveys at randomly selected locations that changed yearly. Areal coverage and sampling spacing on these surveys were similar to plankton cruises. Samples from different surveys, closely overlapping in time and space, were sometimes combined to ensure adequate coverage of the survey area.

Zooplankton was collected with a 61-cm bongo fitted with a 0.333-mm mesh net towed obliquely to a maximum depth of 200 m or 5 m from the bottom and back to the surface. Ship speed varied between 1 and 2 knots to maintain a 45 degree wire angle. Winter surveys in 1977 and 1978 towed bongos at 3.5 knots. A flowmeter was positioned in the center of the bongo frame to measure volume of water filtered during the tow. Samples were preserved in 5% formalin. At all stations, sea-surface temperature was measured with a stem thermometer to the nearest 0.1°C. Detailed sampling procedures, cruise tracks, and survey logistics are summarized by Sibunka and Silverman (1984, 1989).

Biomass was measured by displacement volume in the laboratory. Initially, organisms larger than 2.5 cm were removed. The plankton sample with preserving liquid was then measured in a graduated cylinder, poured through a mesh cone into a second cylinder, and drained until the interval between drops from the cone increased to 15 seconds. The liquid in the second cylinder was measured and the displacement volume of the sample was the difference between readings. Samples with high concentrations of gelatinous organisms were eliminated because the interstitial water retained by these animals leads to gross overestimates of zooplankton biomass. Samples were later subsampled by aliquoting to about 500 organisms and identified to species. Volumes (n=1937) are expressed as cc/100 m^3 of water filtered, and abundance (n=1839) as number/100 m^3.

The adults and late stage copepodites of the copepods *Calanus finmarchicus, Pseuducalanus minutus, Centropages typicus, Centropages hamatus,* and *Metridia lucens* were the dominant species analyzed. Depth distribution of biomass and species abundance was examined by subsetting the data into three geographic subareas according to bottom depth: 1) central shoal (<61 m); 2) intermediate (61–100 m); and 3) deep (>100 m). Seasonal shifts in biomass and community structure were investigated by grouping the data into the six seasons defined in Table 1. Extenuating circumstances prevented adequate areal coverage in only one season: winter 1979.

The Shapiro-Wilk test for normality was applied to each seasonal biomass and species data set. The null hypothesis that the data values were a random sample from a normal distribution was rejected (P<0.01). Zooplankton data are often log transformed to normalize zooplankton distributions. However, Roesler and Chelton (1987) found that transformation of zooplank-

Table 1

Seasonal median values of biomass and dominant species abundance by year and for all years combined during A) Winter, B) Early Spring, C) Late Spring, D) Summer, E) Early Autumn, and F) Late Autumn. *Centropages hamatus* abundance numbers are only from the central shoal depth area and *Metridia lucens* ones are restricted to the deep water depth area. Midpoint refers to the median day number of that years sampling. A '—' indicates no data were collected or processed.

A: Winter (1 Jan.–23 Mar.)											
Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	51	61	—	62	64	66	20	18	17	34	48
Biomass	7	20	—	9	10	9	10	12	8	9	9
C. finmarchicus	1170	1523	—	2814	5539	1531	508	1191	639	1023	1258
P. minutus	1419	8678	—	1746	4814	3157	1131	1685	1701	954	2120
C. typicus	10	263	—	1253	145	2648	2988	1735	3720	2057	976
C. hamatus	0	77	—	1626	0	16	5709	1770	3021	10379	188
M. lucens	121	884	—	154	4334	1422	766	1112	340	49	444
B: Early spring (24 Mar.–4 May)											
Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	115	105	101	102	112	116	103	95	92	104	101
Biomass	86	50	66	43	43	29	36	14	54	76	42
C. finmarchicus	44912	—	22680	15659	36957	27511	17600	5192	6729	19261	18100
P. minutus	19299	—	4483	7217	17032	17098	10654	3339	2449	4600	7217
C. typicus	0	—	1031	353	261	1300	89	34	108	182	207
C. hamatus	306	—	65	3889	549	115	4538	16	1702	10722	569
M. lucens	1666	—	5117	5210	4164	4373	213	1645	567	468	1621
C: Late spring (5 May–22 June)											
Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	157	140	144	168	152	141	168	149	133	153	147
Biomass	137	89	95	42	50	37	15	38	46	21	50
C. finmarchicus	89437	59030	22748	15895	12429	20887	4590	15622	11221	9088	18255
P. minutus	43677	19034	19467	13727	19595	10765	2742	6853	4597	2833	9313
C. typicus	0	0	511	829	356	1274	0	0	0	9	51
C. hamatus	453	0	201	21188	21065	697	26190	13910	34157	7476	2657
M. lucens	8612	9147	24391	9963	2728	13486	117	1145	823	409	2568
D: Summer (23 June–12 Sept.)											
Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	230	206	217	213	198	206	233	233	230	238	202
Biomass	43	37	43	33	46	15	25	25	16	25	31
C. finmarchicus	21856	5346	4737	4556	4667	875	5029	4693	2913	3473	4042
P. minutus	12205	8109	4655	5661	12908	5175	6328	1980	4354	7704	5776
C. typicus	7561	6739	11201	3416	4264	1678	22659	8954	6113	11225	6456
C. hamatus	9958	66547	89476	33095	97265	39490	27922	63458	67507	40335	46140
M. lucens	4040	635	12195	1879	1315	6280	1089	390	9	78	1597
E: Early Autumn (13 Sept.–9 Nov.)											
Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	308	289	297	293	295	302	292	289	297	289	294
Biomass	33	30	30	33	22	19	15	22	32	9	24
C. finmarchicus	638	912	591	282	679	1364	429	454	971	347	587
P. minutus	5986	3472	2284	39	1285	3089	291	220	475	536	898
C. typicus	35103	33342	39431	39256	36453	11784	14322	18970	71184	5124	28431
C. hamatus	25608	17018	49178	10833	13524	14138	2024	17480	15068	5765	14138
M. lucens	2180	1020	4332	1895	3227	49	257	71	27	28	540
F: Late Autumn (10 Nov.–31 Dec.)											
Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	327	330	337	350	337	325	344	333	338	339	334
Biomass	22	23	24	11	13	27	7	12	18	6	16
C. finmarchicus	1186	573	133	683	419	1137	812	711	538	78	539
P. minutus	13752	7922	942	1826	799	2169	540	187	198	388	1030
C. typicus	17960	33013	24117	9200	21241	15835	9209	15646	50081	2594	16378
C. hamatus	4739	1691	23626	345	3999	21416	6057	24439	45741	10759	5523
M. lucens	1742	1570	7058	4773	4503	870	243	385	263	12	735

ton biomass can screen important biological events by repressing anomalous values. Therefore, nonparametric statistical techniques were employed to test for differences between years within the defined seasons. The Kruskal-Wallis ANOVA was used to determine if significant ($P<0.05$) differences existed between years within each season. The test showed that all biomass and species seasonal groupings had at least one pair of years different from each other. The Dunns multiple comparison procedure was applied to pinpoint the anomalous year(s).

Results

Annual cycle

Median biomass and dominant copepod abundance values for each of the defined seasons by year and for the ten-year study period are given in Table 1, A–F.

Biomass on average increased fourfold in early spring from its winter low. It peaked in late spring and then gradually declined through the summer and autumn seasons (Fig. 2). Overall, zooplankton standing stock was high from 1977 through 1979. Seasonal medians from early spring through late autumn were above time-series median values (Fig. 2A). The opposite pattern was evident from 1982 through 1984. Zooplankton standing stock was below average throughout these years, except for late autumn 1982 (Fig. 2B). Winter biomass showed little variation throughout the study period (Table 1A).

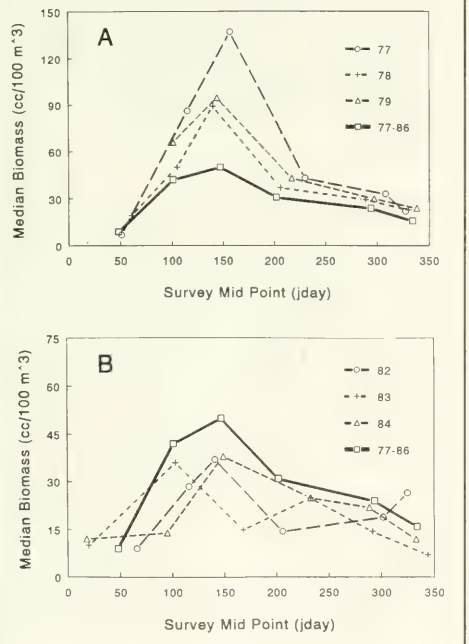

Figure 2

(A) Annual cycle of seasonal median biomass values in 1977 through 1979 and the ten-year median. **(B)** Annual cycle of seasonal median biomass values in 1982 through 1984 and the ten-year median.

The seasonal biomass cycle on Georges Bank from 1977 through 1981 was coherent; annual departures from the mean were insignificant (Sherman et al., 1983). However, substantial departures from the average seasonal cycle occurred on several occasions after 1981. Surveys in 1983, 1985, and 1986 recorded peak biomass in early spring instead of late spring and in two of those years, 1983 and 1986, there was an anomalous increase in biomass during the summer months (Fig. 3). However, because only below average summer levels were reached during these years, the latter increases appear to represent a recovery from the minimal levels measured in late spring, rather than a summer bloom. Zooplankton standing stock increased between summer and early autumn in only two years: 1982 and 1985 (Table 1, D–E). The usual decline in biomass between early and late autumn was not observed in 1982 (Table 1, E–F).

The average ten-year seasonal distribution of each variable as a function of bottom depth is depicted in Figure 4. There were no apparent long-term distribution shifts in biomass or species abundance during the ten-year period.

Calanus finmarchicus and *P. minutus* both dominated the zooplankton community in early and late spring. During the summer, their populations declined and *C. typicus* began to increase in abundance until it peaked in early autumn (Table 1). *Centropages hamatus* and *M. lucens* were only prevalent in specific depth strata (Fig. 4). *Centropages hamatus* was almost entirely restricted to the central shoal depth region, peaking there during summer months. *Metridia lucens* was most numerous in deep water where its large size caused it to be a major contributor to spring biomass. Overall, it was the only dominant species that exhibited a long-term abundance trend. Population estimates for *M. lucens* were low in 1983 through 1986 (Table 1).

All the above species showed departures from their average seasonal cycles during their periods of peak abundance. *Calanus finmarchicus, M. lucens,* and *P. minutus* all declined between early and late spring in 1983 and 1986 (Table 1, B–C). *Centropages typicus* departed from its typical annual abundance pattern during three years; population estimates in 1983 and 1986 declined from summer to early autumn and in 1982, *C. typicus* did not reach peak abundance until late autumn. The *C.hamatus* population was more variable than the other species. From 1977 to 1981, abun-

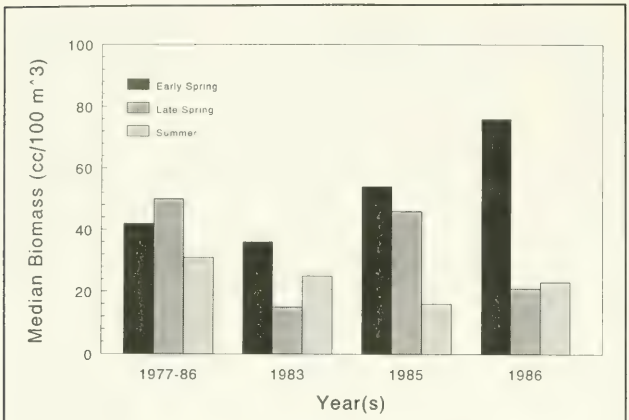

Figure 3
Departures from the ten-year (1977–86) median biomass cycle occurred between early spring and summer in 1983, 1985, and 1986.

dance decreased from early to late autumn. During the next five years, increases were recorded between seasons (Table 1, E–F). After an unusual pulse in early spring 1986 (Table 1B), *C. hamatus* declined in late spring and then rebounded to their average summer abundance. In one year, 1977, its annual high was delayed until early autumn (Table 1, D–E).

Surface temperature variability was examined by fitting seasonal medians (Table 2) to a harmonic regression (Fig. 5). The model depicted a strong annual cycle; $r^2 = 0.91$. Certain seasons in specific years had above or below average temperatures, but there were no prolonged warm or cool periods.

Interannual variability by season

Winter Zooplankton standing stock reaches its annual low and exhibits little interannual variation during the cold winter months (Table 1A). The only remarkable year was 1978, when median biomass was nearly double all other years. However, this may have been an artifact of survey logistics, rather than enhanced winter productivity. None of the usually low biomass stations along the northern and southern perimeter of Georges Bank were sampled that year.

Centropages hamatus was the only dominant species that demonstrated substantial interannual variation during the winter season. Population estimates in the central shoal depth zone from 1983 to 1986 were well above the ten-year median (Table 1A). These departures can be directly related to surface-temperature variability caused by dates of survey coverage. Throughout the winter time series, *C. hamatus* was virtually absent at stations where surface temperature was below 5°C (Fig. 6). Median surface temperatures for the years 1983–86 were all above 5°C (Table 2) and significantly higher ($P<0.05$) than the earlier years, which were all sampled later in the season when the annual minimum temperature on Georges Bank is normally reached. Biomass and the abundance of the other four copepod species were not affected by winter temperature regimes.

Early spring Zooplankton biomass in early spring was high at the beginning and end of the time series; 1977 and 1986 (Table 1B). Standing stock in 1984 was very low; significantly less ($P<0.10$) than all other years except 1982.

C. finmarchicus and *P. minutus* abundance (Table 1B) was similar to biomass trends in some years. Like biomass, abundance estimates for both species were highest in 1977 and low in 1984. In 1986, an unusual early spring pulse of *C. hamatus* (Table 1B) in the central shoals depth area elevated standing stock levels. The above average biomass levels recorded in 1985 could not be related to the low abundance estimates of the dominant species in that year (Table 1B). Notations made by shipboard personnel indicated that nets were frequently clogged with dense concentrations of phytoplankton. High biomass in 1985 was likely elevated by phytoplankton and entrapped organisms not usually captured with 0.333-mm mesh nets.

As in winter, the C. *hamatus* population was depressed by cold temperatures in early spring. Their highest early spring abundance occurred in 1986 when surface waters in the central shoals depth area were warmest (median=6.5°C) in this season. *Calanus finmarchicus* were also more abundant at stations where surface temperatures were 6°C or more. Annual changes in biomass and the abundance of other dominant species could not be related to surface temperature variability in early spring (Table 2).

Late spring Zooplankton biomass surged in the late spring of 1977 (Table 1C). The median volume was nearly three times higher than the seasonal 10-year median, and significantly different ($P<0.05$) from all years except 1978 and 1979. Though biomass declined from this peak in 1978 and 1979, median estimates in these two years were nearly double those recorded in

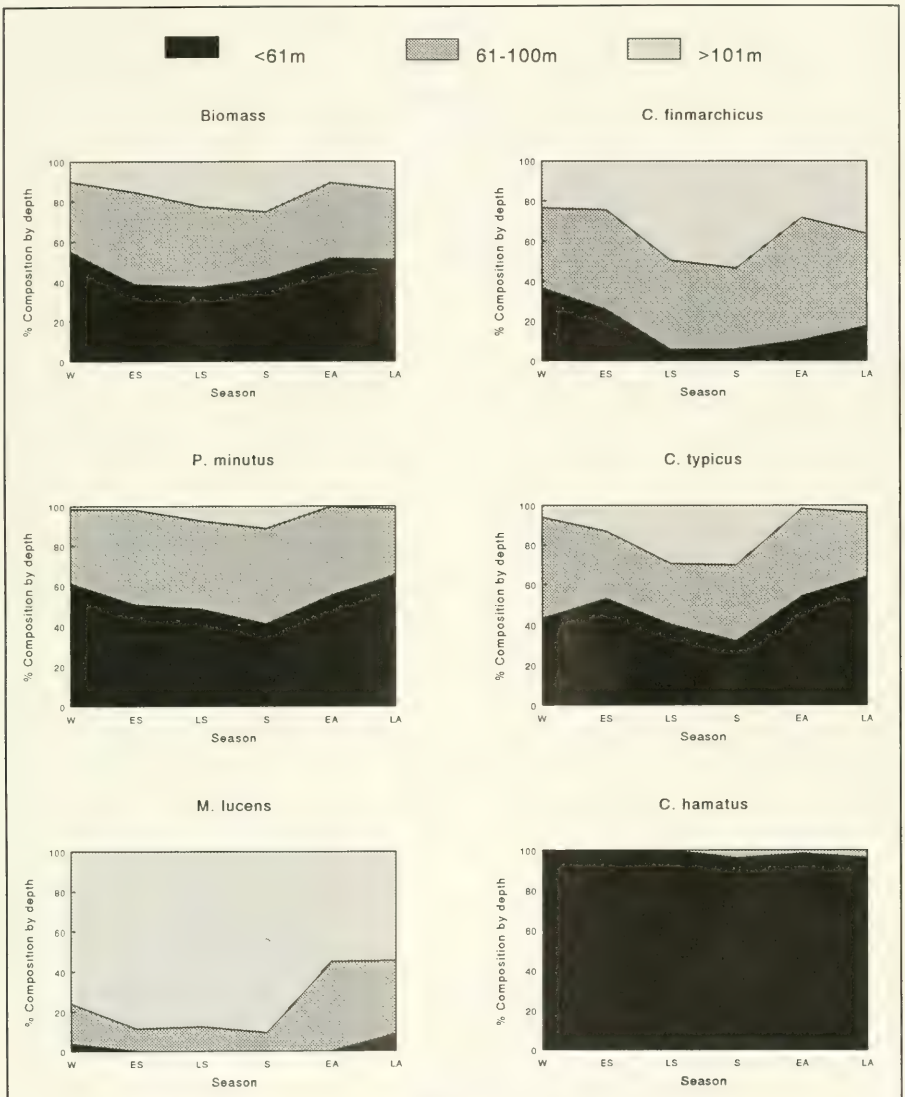

Figure 4

The average seasonal distribution of biomass and the five dominant species as a function of depth during the ten year study period. Season abbreviation key: W = Winter, ES = Early Spring, LS = Late Spring, S = Summer, EA = Early Autumn, and LA = Late Autumn.

the 1980's. Extremely low estimates were recorded in 1983.

Interannual fluctuations in late spring biomass were closely related to *C. finmarchicus* and *P. minutus* abundance (Table 1C). The similarities between abundance plots of both species during spring seasons (Fig. 7) suggest that their population dynamics may be controlled by similar factors.

Table 2

Seasonal median sea surface temperature (°C) by year and for all years combined. No data were collected in Winter 1979.

	Year										
Season	77	78	79	80	81	82	83	84	85	86	All data
Winter	4.9	4.6	—	4.8	4.2	3.4	7	5.7	6.9	5.7	5.2
Early spring	6.6	4.7	4.7	5.7	5.6	5.2	6.2	5.2	5.4	6	5.5
Late spring	9.6	7.4	8.5	11.6	10.2	7.2	10.4	8.9	7.9	9.2	9.1
Summer	16.4	14.7	16.7	18.1	15.0	15.6	16.1	18.2	16.8	15.3	16.1
Early autumn	14.0	13.5	14.4	14.9	12.5	12.9	14.3	14.1	13.8	13.6	13.6
Late autumn	10.6	11.6	10.4	7.4	9.9	11.5	9.2	10.8	9.8	10.6	10.2

There were two notable annual distribution shifts in late spring. *Calanus finmarchicus* abundance was usually sparse within the 60-m contour and evenly distributed offshore of it (Fig. 4). However, in the high biomass years of the late 1970's, the population thrived in central shoal waters. From 1977 to 1979, *C. finmarchicus* medians were 48,366, 33,397,and 15,364/100 m^3 respectively, while other years were all below 5000/100 m^3. *Metridia lucens* abundance in deep water peaked in 1979 (Table 3C) and they extended their range of dominance inshore across the 100-m contour line. Its high abundance (median = 22,015/100 m^3) in the intermediate depth zone, where its 10-year median was 365/100 m^3, elevated biomass there to nearly double the time-series median, despite only average *C. finmarchicus* abundance. The *M. lucens* abundance peak in 1979 accounts for the high biomass measured in that year.

Centropages hamatus was the dominant copepod species in the central shoals area during 1980 and 1981 and from 1983 to 1986. In other years, their numbers were sparse there; median values fell below 1000/100 m^3 (Table 1C). Their high years correlated with all but one (1981—*P. minutus*) of the low abundance years for *C. finmarchicus* and *P. minutus* (Fig. 8).

The strongest relationship between abundance and surface temperature variability in late spring (Table 2) was for *C. hamatus* numbers in the central shoals area. Five of the six years, during which they dominated those waters, temperatures were warmer than average, and three of the four years in which they were sparse were below the ten-year median temperature. Biomass and other dominant species abundance could not be related to interannual differences in median surface temperatures.

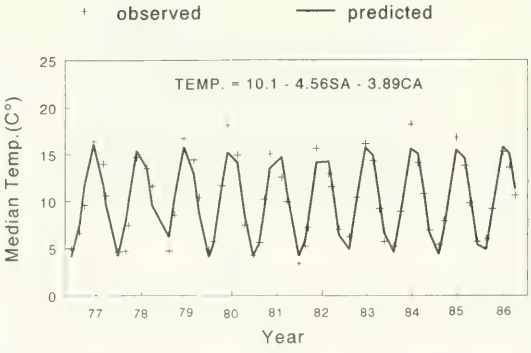

Figure 5

Seasonal median surface temperatures and the ones predicted from the harmonic regression model. Terms in the model are defined as follows: CA = Cos(0.0172*sampling midpoint(jday)); SA = Sin(0.0172*sampling midpoint(jday)).

Summer The spring zooplankton biomass surge of the late 1970's continued through the summer months. Biomass levels in those years and in 1981 were significantly different ($P<0.05$) from the low measures obtained in 1982 and 1985 (Table 1D).

Centropages hamatus was prevalent in the well mixed central shoals, but Georges Bank as a whole was not dominated by one copepod species during summer months (Table 1D). Biomass in 1977 was elevated when *C. finmarchicus* and *P. minutus* abundance reached near seasonal highs during the ten-year period. Notable in 1977 was that *C. hamatus* numbers in shallow water were minimal and *C. finmarchicus* abundance there (8386\100 m^3) was at its summer high, reinforcing the inverse abundance relationship observed between them in late spring. As it did in late spring, high *M. lucens* abundance outside the 60-m isobath raised biomass in 1979. Its abundance within the intermediate depth zone (4193\100 m^3) was well above its 10-year median there of 167\100 m^3. Biomass in 1981 was raised when both *P. minutus* and *C. hamatus* abundance estimates reached

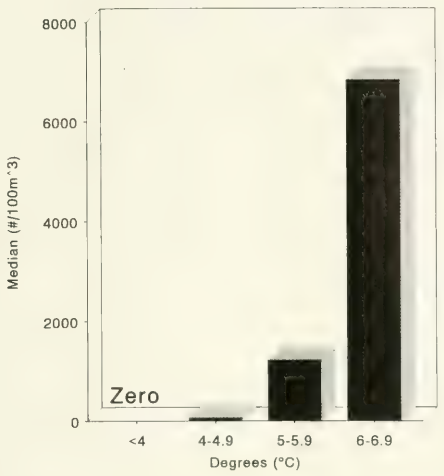

Figure 6

Ten-year median abundance of *Centropages hamatus* during the winter season at 1°C surface temperature intervals. Population estimates are from the central shoal depth area only.

seasonal highs for the ten-year period. *Calanus finmarchicus, P. minutus,* and *C. typicus* were all below average abundance in the low biomass years of 1982 and 1985.

No strong correlation between median surface temperatures and biomass was evident during the summer. *Calanus finmarchicus* abundance estimates were highest at stations where surface temperatures had warmed above 17°C, reflecting their shift to warmer waters outside the 100-m isobath in summer (Fig. 4). This relationship is probably related to the cooler water found below the seasonal thermocline (Manning and Holzwarth, 1990), rather than to the warm surface layer where this cold water species is unlikely to concentrate. Abundance of other species was variable over the range of summer temperatures.

Early autumn Four high biomass years, from 1977 to 1980, were followed by diminishing ones through 1983 (Table 5E). Biomass began to climb in 1984 and again reached high levels in 1985. Standing stock fell to its lowest level in 1986. The depth distribution of the high biomass of 1980 differed substantially from average conditions (Fig. 4). Median biomass from the intermediate (39 cc/100 m^3) and deep (30.5 cc/100 m^3) water zones

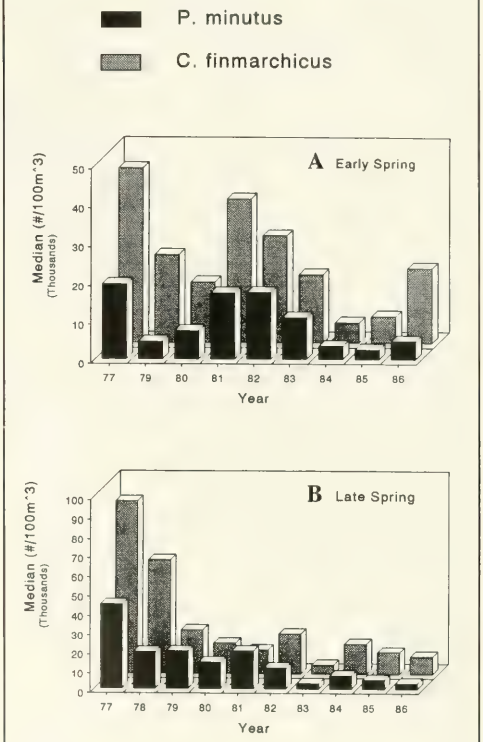

Figure 7

Median abundance of *Calanus finmarchicus* and *Pseudocalanus minutus* in 1977 through 1986 during **(A)** early spring and **(B)** late spring.

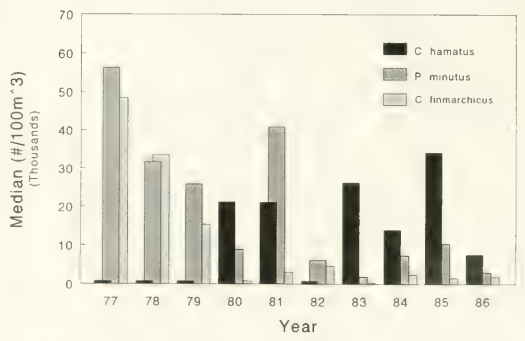

Figure 8

Median late spring abundance of *Centropages hamatus, Calanus finmarchicus,* and *Pseudocalanus minutus* in the central shoal depth region in 1977 through 1986.

were both higher than those from the central shoals area (27 cc/100 m^3), the region where biomass is usually concentrated.

Centropages typicus dominates the zooplankton population in early autumn; it makes up on the average 41% of total zooplankton abundance. Consequently, variation in its interannual abundance pattern nearly mirrored that of early autumn biomass. The only substantial deviation between patterns occurred in 1985 when *C. typicus* density soared to its ten-year high (Table 1E). Biomass was high in early autumn 1985, but not in proportion to this copepod's abundance. *Centropages typicus* abundance usually declined substantially offshore of the 100-m contour (Fig. 4). However, its abundance (10,805/100 m^3) in the deep-water depth area in 1980 was substantially higher than the time series median (1319/100 m^3). Consequently, offshore biomass in 1980 (30.5 cc/100 m^3) was also well above the deep-water 10-year median (7 cc/100 m^3). Though their numbers decline from summer, *C. hamatus* abundance continues to be a large component of zooplankton biomass in central shoal waters. Population estimates peaked in 1979 and, like biomass, were low in 1986 (Table 1E). Early autumn departures from average annual or seasonal cycles of biomass and species abundance and distribution could not be related to variations in surface water temperature (Table 2).

Late autumn The high zooplankton biomass of the late 1970's continued through late autumn (Table 1F). The seasonal peak recorded in 1982 was unexpected. Biomass increased from early autumn and pushed 1982 measurements above average for the first time. These high years were all significantly different ($P<0.05$) from the seasons lowest biomass measured in 1983 and 1986, the same years that were low in early autumn.

Centropages typicus continue to dominate the zooplankton as biomass declined towards its winter low. Its abundance was above average in the high biomass years of the late 1970's (Table 1F). The high biomass of 1982 was not related to total copepod or zooplankton numbers. Median counts of the five dominant copepod species and total zooplankton were not significantly different ($P>0.05$) from any of the other years. Cursory examination of other species abundance indicated that chaetognaths were prevalent and may have increased the biomass. The reverse occurred in 1985 when slightly above average biomass did not correlate to high zooplankton abundance. *C. typicus* and *C. hamatus* abundance in late autumn 1985 were three or more times above the ten-year median (Table 1F).

Warm late autumn temperatures appear to slow the decline of zooplankton biomass and abundance to the annual lows found in winter. High biomass years in late autumn all had above average surface temperatures (Table 2). The only high biomass levels of early autumn that were not sustained through late autumn were those collected in 1985, when surface temperature had fallen below the ten-year median. Consequently, it is not surprising that biomass and dominant copepod abundance were highest at stations where surface temperature was warm. The bimodal annual cycle displayed by *C. hamatus* in the mixed depth zone, that is to say the decline in numbers between early and late autumn from 1977 to 1981 and the increase in subsequent years (Table 1, E–F), cannot be explained by variability in autumn surface temperatures.

Discussion

The zooplankton population on Georges Bank exhibited considerable interannual and seasonal variability during the period from 1977 to 1986. Overall, biomass was above average from 1977 through 1979 and low from 1982 through 1984. Unique to the late seventies was the high late spring abundance of *C. finmarchicus* in the central shoal depth zone. The species was only a minor component of the zooplankton community there in later years. Compared with other years, 1977 biomass and copepod abundance levels in spring were extraordinary: two to three times above the ten-year median.

Calanus finmarchicus and *P. minutus* abundance fluctuations were nearly identical throughout the ten-year time series. This suggests that the annual abundance of these two species is regulated by similar processes and events, despite differences in their life cycles (Davis, 1987). This is in contrast to the results derived by Davis (1984) from model simulations of their seasonal cycles on Georges Bank. He concluded that predation pressure alone controls *P. minutus* population levels and that *C. finmarchicus* is regulated by both predation and food availability. The data presented here indicates that its unlikely that these species have different factors limiting their annual abundance. Furthermore, preliminary studies indicate that abundance estimates of both species on Georges Bank are correlated to chlorophyll levels in the water column[1]. Investigations on *P. minutus* population dynamics should not exclude food supply as a potential limiting factor.

Centropages hamatus abundance estimates were more variable and temperature sensitive than those for other dominant copepod species. Of special interest is that *C. hamatus* spring abundance pulses were inversely related to both *C. finmarchicus* and *P. minutus* population estimates. It is unlikely that temperatures which stimulate *C. hamatus* production would be detrimental to *C. finmarchicus* or *P. minutus*. Laboratory

[1]C. Meise, National Marine Fisheries Service, Narragansett, RI 002882, unpubl. data.

studies (Marshall and Orr, 1955; Corkett and McLaren, 1978) have shown that both *C. finmarchicus* and *P. minutus* grow and reproduce within the upper range of spring temperatures. There was no evidence in our data that either species had a strong response to spring surface temperature variability. One possibility is that the omnivorous *C. hamatus* may have depressed production in the other species by preying on their egg and naupliar stages, as Davis (1984) suggests they do in autumn months. Physical or behavioral responses to other changing spring conditions, such as daylight or thermocline formation, cannot be eliminated as potential factors that triggered or limited their production.

There is growing evidence that the earth's climate is changing (Mitchell, 1989). The impact of global warming on Georges Bank zooplankton could be substantial because the area is a faunal transition zone between northern boreal species and southern warm water plankton (GLOBEC, 1991). The sensitivity of the Georges Bank *C. hamatus* population to temperature indicates that the effects of a long-term warming trend might first affect the life cycle of this species. *Centropages hamatus* virtually disappears from the water column when surface temperature falls below 5°C. Marcus (1989) has shown it produces diapause eggs and reports that nauplii appeared after incubation of Georges Bank sediment. *Centropages hamatus* apparently overwinters as bottom resting eggs that hatch when water column temperatures rise to some threshold. If this phase of its life cycle is shortened or eliminated by global warming, growth and reproduction in the central shoals could continue year round and potentially limit the production of other copepod species. The early to late autumn rise of *C. hamatus* abundance from 1982 to 1986 suggests dormancy was postponed and an additional generation produced in these years. Since monthly anomalies of sea surface temperature for 1981–86 in the area indicate a warming trend (Wood and Tang, 1988), this may be the first signal that climatic change is affecting the marine ecosystem.

Interannual variability in the amount of food available to larval fishes is believed to be an important determinant of their survival and subsequent recruitment to adult populations. Field evidence for the linkage between larval survival and zooplankton prey concentrations is poor (Laurence and Lough, 1984; Leak and Houde, 1987). Though this report was not designed to examine the relationship between zooplankton variability and its effect on fishery resources on Georges Bank, it should be noted that zooplankton biomass patterns closely resembled those of northern sand lance (*Ammodytes dubius*) population estimates. Their population surged in the late seventies, responding to a reduction in predation and competition pressure caused by the fishery-induced collapse of herring and mackerel populations (Sherman et al., 1981). Relative abundance of the zooplanktiverous sand lance in survey trawls increased dramatically between 1977 and 1981, decreasing thereafter through 1986 (Nelson, 1990). The sand lance explosion may have been fueled by the high concentrations of zooplankton food stocks available in the late 1970's.

Interannual variations in time of sampling can bias estimates of biomass and abundance for predefined seasons. Early spring on Georges Bank is especially sensitive to this bias because the zooplankton population is beginning to harvest the late winter phytoplankton bloom and is rapidly transferring it to higher levels of the food chain. Obviously, the calendar definition of early spring used here to subset data may not be real in nature. The question arises whether the biomass estimates recorded in early spring 1984 were truly low or was sampling conducted too early? Median surface temperature in 1984 was only 0.3°C below the ten-year median of 5.5°C. There were other years with lower temperatures that had higher estimates of biomass. A biological sign of spring's arrival on Georges Bank is the presence of early copepodite stages of *C. finmarchicus* in the water column. The spring phytoplankton bloom triggers their spawning and, if spawning had not yet occurred, only overwintering stage-5 copepodites would be present (Davis, 1987). However, in 1984, 52.7% of the population was stage-2 and stage-3 copepodites, similar to the high biomass year of 1977 where 56.2% of the population were these early developmental stages. Thus, the low zooplankton biomass measured in early spring 1984 was probably real.

There is presently only a perceptual understanding of how physical processes affect the abundance and distribution of Georges Bank zooplankton. The success of a population depends not only on food availability and predator abundance but also upon the dynamics of its physical environment, which influence feeding efficiency, susceptibility to predation, transport, and recruitment success. Sea-surface temperature was the only physical parameter discussed in this report and its narrow range of variability could not be correlated to the comparatively large fluctuations of the zooplankton population. Monthly mean-derived wind stress components in the area (see Ingham and Wood, 1987) and anomalies in the volume of Georges Bank shelf water (Mountain, 1991) were also examined from 1977 to 1986 and no persistent correlation to biomass variability was evident. Ongoing studies are presently analyzing historical time series of physical and biological parameters to help direct future research efforts attempting to couple the physics and biology of the marine environment. Future monitoring surveys of the U.S. Northeast shelf ecosystem will continue to measure the variability of zooplankton and gather infor-

mation to identify the key environmental and physical factors that drive their population dynamics.

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Spatial structure and temporal continuity of the South Georgian Antarctic fish community

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Abstract.—Demersal fish represent one of the most heavily exploited resources in the Antarctic ecosystem. The stocks around South Georgia Island have contributed a substantial portion of the annual catches and have declined over the past decade. Fishing has been implicated as the cause of this decline. However, a clear description of the community structure of this system, which is necessary to judge the influence of fishing accurately, has been lacking.

The spatial structure of the South Georgian fish community was investigated through the use of survey data collected over a three-year period. The results clearly indicated the absence of spatial structure in that community. The presence or absence of rare species at various stations was responsible for the weak structure found in the initial analysis. The general lack of structure was consistent from year to year.

The available data do not provide an explanation for this lack of structure. All surveys were conducted during the austral summer only. Events and community structure at other times of the year remain unknown. Although the data were representative of the fish community during the austral summer, no comparable data were available on the abundance and distribution of their prey items, especially krill (*Euphausia superba*). More extensive sampling, expanded to include other seasons, is necessary to properly address the questions of seasonal change in community structure and the role of competition in this Antarctic system.

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The marine systems of the Antarctic are important both ecologically and economically. Many of the seasonal and long-term events that occur in this region have a significant impact on global environmental conditions (Gordon, 1975; Broecker and Peng, 1982; Kennett 1982, p. 249). The Antarctic is a large region physically isolated from the rest of the globe by the circumpolar circulation of the West Wind Drift Current (Kennett 1982, p. 725). The organisms of the Southern Ocean are unique and often highly productive. The waters south of the Antarctic convergence (about 5% of the world ocean) contribute a total production equivalent to 20% of that produced by all the oceans of the world (El-Sayed, 1968). In fact, it is believed that the evolution of the Mysticeti (baleen whales) depended on the development of the great production of this area (Fordyce, 1977).

The environment of Antarctica and its associated islands has been established for a long time (ca. 37 million years), allowing a group of perciform fishes to radiate into a variety of niches and to dominate the fish fauna of this highly productive region (DeWitt, 1971; Targett, 1981; Eastman, 1985). Like other polar communities it is one of low species richness (Hedgepeth, 1969; Everson, 1984). Over 70% of the species and 90% of the individuals belong to four families in the suborder Notothenioidei and 95% of the species in this group are endemic to the Antarctic region (DeWitt, 1971). The four dominant families are the Antarctic cods (Nototheniidae), dragonfish (Bathydraconidae), icefish (Channichthyidea), and plunderfish (Harpagiferidae). These fish are generally sedentary, benthic forms found on the Antarctic continental shelves (Targett, 1981). Many of the species in this group have evolved to fill niches usually occupied by different families or orders of fish (Eastman, 1985).

Large stocks of demersal fish were discovered around some of the islands of the Scotia Arc in the late 1960's (Kock, 1986). A relatively intense and successful fishery developed around these stocks, especially those found at South Georgia Island (Fig. 1). However, the decline of those stocks over the past two decades has been evident (Kock, 1985a, 1986; Gabriel, 1987; McKenna and Saila, 1989; McKenna[1]). This is especially true for the target species of this fishery, the marbled rockcod (*Notothenia rossii*) and the mackerel icefish (*Champsocephalus gunnari*). There is also evidence that a short-term (two to three years) shift in the species assemblage inhabiting the continental shelf around South Georgia has occurred (McKenna and Saila, 1991).

Although overfishing is suspected as the cause of the changes observed

[1]McKenna, J. 1990. Status of the stocks of Antarctic demersal fish in the vicinity of South Georgia Island, January 1989. Antarctic Mar. Living Res. Contract Rep. Available from Dr. R. Holt, NOAA, NMFS, Southwest Fisheries Sci. Center, La Jolla, CA 92038.

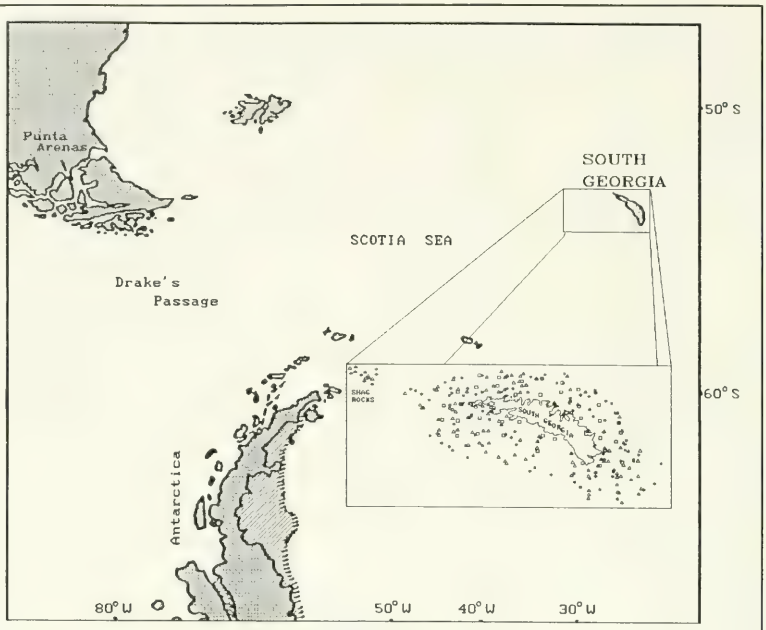

Figure 1

Map showing the location of South Georgia Island in the Southern ocean. Inset map identifies samples sited during each of the three AMLR cruises. Each asterisk (*) represents a sample taken during the 1986–87 survey. Each triangle (△) represents a sample taken during the 1987–88 survey. Each square (□) represents a sample taken during the 1988–89 survey.

in the demersal fish community (Kock, 1985b, 1986, 1991; Kock and Koster, 1989, 1990), there is a need for more basic information about the ecology of these fishes. The effects of natural (or anthropogenic) events on the populations of these animals cannot be accurately judged without a clear understanding of their basic community organization.

Analysis of Antarctic fish communities has generally been limited to descriptions of the species present and some investigations of their diets. Targett (1981) included some measures of diversity in his examination of the fish community at three different islands along the Scotia Arc. His research emphasized diets and resource partitioning, and gives some of the first descriptions of relationships between the species based on a quantitative analysis. However, his sampling was limited to one or two locations at each island. More extensive work has been conducted at Elephant Island by Tiedtke and Kock (1989). Their examination of the demersal fish assemblage around that Island found evidence of spatial structure associated with depth.

A survey program concentrating on the South Georgia area was established as part of the U.S. Antarctic Marine Living Resources (AMLR) project. The research described here used the data from that program to examine the spatial structure of the demersal fish community in the vicinity of South Georgia Island and its temporal consistency from 1986 to 1989.

Methods

Data used in this study consisted of species abundances (and associated length-frequency information) collected during three research survey cruises in the South Georgia area. The abundance of each species in the region was measured both numerically (number/standard tow) and on a biomass (kg/standard tow) basis.

These surveys were conducted during the austral summers of 1986–87 (29 Nov.–17 Dec. 1986), 1987–88 (19 Dec.–10 Jan.), and 1988–89 (17–28 Jan. 1989). The 1986–87 and 1987–88 surveys sampled the abundance

of fish from approximately 100 stations (Fig. 1) by thirty minute tows of a P32/36 otter trawl (mouth opening of 17.5 m, 43–52 mm mesh liner). These stations had been randomly located within three depth strata (50–150 m, 150–250 m, 250–500 m) (Gabriel, 1987; McKenna and Saila, 1989). The 1988–89 survey sampled 41 stations from a regular grid between 50-m and 250-m depth around South Georgia Island (Fig. 1). Collections of demersal fish during that survey were made with fifteen minute tows of a Christensen Bottom Trawl (wing spread of 4.6 m, 50-mm mesh codend with a 6-mm liner)(McKenna[1]). Complete discussions of the methods and results of these surveys may be found in Gabriel (1987), McKenna and Saila (1989), and McKenna[1].

Species diversity has become a standard tool for describing natural communities. Three measures of diversity were calculated for each station sampled during the three surveys and for each survey as a whole based on the total catches. The first was species richness, which was simply the number of species caught at each station. The second was the Shannon-Wiener information index (H', using loge) (Shannon and Weaver, 1949). The third index (V) was a measure of evenness (Pielou, 1977),

$$V = H'/\log(s^*),$$

where s^* is the total number of species in the region and was assumed to be 30.

Species associations give a more detailed description of a natural community than the simple summary provided by diversity indices. Species associations within each survey were identified by use of Spearman rank correlation (r') analysis (Freund, 1970, p. 311–313), and were based on the numerical abundance of fish caught during each survey. Species were arbitrarily designated as rare if they occurred at 5% or less of the sampled stations and uncommon if they occurred at 25% or less of the stations sampled. All pairwise combinations of common species (within each season) were examined. These correlation values were then used to generate Z-scores ($Z = r'\sqrt{(n-1)}$) to test the null hypothesis that the correlation was not significantly different from zero. Significance of associations was determined at the 0.01 level ($Z \geq 2.58$) (Freund 1970, p. 313).

Cluster analysis was used to examine the spatial structure of the community in an effort to identify significant subcommunities. This analysis method reduces the complex, multivariate data from field studies to a manageable level (Boesch, 1977) and often reveals the presence of important physical or biological factors affecting the distribution of the various species assemblages occupying the sampled region (Pielou, 1977). However, one of the major drawbacks of cluster analysis (and many other exploratory techniques) is the subjectivity associated with its application (Boesch, 1977; Pielou, 1984; Jain and Dubes, 1988).

The heterogeneity ratio (HR) was used in this analysis as the measure of similarity for the normal (R-mode) cluster analyses, because of the objectivity it provides. It is not affected by sample size or group size (the number of samples included in a cluster), measures the beta-diversity (McNaughton and Wolf, 1979a) existing among samples, and can be statistically tested for significance (Kobayashi, 1987).

$$HR = S_Q/E(S_Q),$$

where S_Q is the total number of species present in Q samples and $E(S_Q)$ is the expected number of species in the Q samples. $E(S_Q)$ is obtained by applying the mean number of species per sample to the logarithmic series distribution (Fisher et al., 1943), which is used as the model describing the relation between the sample size and number of species in the community. The logarithmic series describes communities which are dominated by one or a few species and contain numerous rare species. It is a common distribution in nature (Shepard, 1984; Dial and Marzluff, 1989) and is the most appropriate for this application (Kobayashi, 1987).

HR is robust to the requirement of good fit to the logarithmic series model (Kobayashi, 1987). However, the fit of the data to that distribution was tested for each station sampled during the three surveys with the aid of the BASIC program LOGSRFIT.BAS (Saila et al., 1991). This program generates values of X, Fisher's α, and K. X and α are the parameters of the logarithmic series model and α is also a diversity index (Fisher et al., 1943; Saila et al., 1991). Values of K measure the goodness-of-fit of the data to the logarithmic series model (Fisher et al., 1943). Values of K less than 1.0 indicate a reasonable fit to the model.

A normal (R-mode) clustering of the stations was performed for each survey. The clustering program, HRCLUSTR.BAS (written in Microsoft QuickBasic v. 4.5, Microsoft 1988), was developed for this purpose (available upon request). It was a modification of Kobayashi's[2] program and used the HR and an unweighted paired group method of averaging (UPGMA) linkage method (Sneath and Sokal, 1973). The null hypothesis of non-significant clusters was rejected at the 0.05 level (Kobayashi, 1987). Inverse (Q-mode) clustering was also preformed on each survey's data to classify species into groups. This provides insight into

[2]Kobayashi, Faculty of Agriculture, Yamagata Univ., Tsuruoka, 997 Japan. Pers. commun. 1988.

their associations and distributions. The species were clustered with the correlation coefficient and an UPGMA linkage method (Jain and Dubes, 1988, p. 16). The results of these analyses were then combined through nodal analysis (Williams and Lambert, 1961; Lambert and Williams, 1962; Noy-Meir, 1971; Boesch, 1977) into two-way tables displaying the constancy and fidelity of the identified groups (Fager, 1963; Westhoff and van der Maarel, 1973).

Constancy describes how widespread a species group is within a given habitat and is expressed as

$$C_{ij} = a_{ij}/(n_i n_j),$$

where a_{ij} is the actual number of occurrences of members of species group i in collection (station) group j, and n_i and n_j are the number of entities in the respective groups. C_{ij} ranges from 0 to 1, where 1 indicates that all species occurred in all collections in the group (Boesch, 1977).

Fidelity describes the restriction of a species group to a given habitat and is expressed as

$$F_{ij} = (a_{ij} \sum_i n_j)/(n_i \sum_i a_{ij})$$

Values of this index greater than 2 suggest a strong preference of species in a group *(i)* for a collection group *(j)*, and values much less than 1 suggest avoidance of a collection group *(j)* by a group of species *(i)* (Boesch, 1977).

The size structure of each species' population (1987–88 and 1988–89 surveys only) was also examined for patterns. Stations were clustered (using *HR* and UPGMA linkage) based on the abundance of individuals in each centimeter length class.

Natural communities may be aligned along environmental gradients, changing continuously from one end to the other (Whittaker, 1960). Skewer analysis uses multivariate correlations to measure the significance of linear trends in natural communities (Pielou, 1984; Saila et al., 1991). It was used in this study to examine the significance of trends in each community along suspected gradients of depth, longitude, latitude, and time (date within each survey). It was performed twice on each data set. The first application used the absolute measures of abundance, which detects trends that are a combination of changes in the species assemblage and the absolute abundances of individuals at each station. The second application used those abundance values converted to proportions, which is sensitive only to the changes in species composition along the gradient. Kendall's Tau provided the measure of correlation between each skewer and the observed data. The distribution of Tau was observed through the use of ten classes (0–0.1, 0.1–0.2, etc.). Each data set was sorted in the order of the gradient being examined and probed with 500 skewers. Twenty random tables were generated during each analysis to provide a test of the null hypothesis that the assemblages were distributed randomly along the gradient at a 0.05 probability level (Pielou, 1984).

Although the change in an assemblage along an environmental gradient may be gradual, there may also be cases of rapid change. These ecotones may be due to rapid change in the environmental gradient or possibly a biological change for some other reason (Whittaker, 1960; McNaughton and Wolf, 1979b). Gradient analysis (Webster, 1973; Ludwig and Cornelius, 1987) was applied to the data sorted in order of each of the above potential gradients, to search for boundaries along the length of those gradients. The BASIC program, GRADSECT.BAS (written in Microsoft QuickBasic v. 4.5, Microsoft 1988), was developed for that purpose (available upon request). It used a moving split-window distance method of comparing moving averages (Whittaker, 1960). Each window contained nine stations and the multivariate distance measure was based on the squared Euclidean distance.

Results

The assemblage of demersal fish occupying the South Georgia region, during the three AMLR surveys, consisted of slightly more than two dozen (28) species, with representatives from thirteen families (Table 1). Seven of these species accounted for the vast majority (>85%) of fish biomass and individuals in the system (Fig. 2). Five are relatively large (>50cm), commercially valuable species. These included the three icefish (Channichthyidae) of the region *(Chaenocephalus aceratus, Champsocephalus gunnari,* and *Pseudochaenichthys georgianus)* and two species of rock cod (Nototheniidae: *Notothenia gibberifrons* and *Notothenia squamifrons).* The other two important species *(Notothenops larseni* and *Notothenops nudifrons)* are small but abundant members of the Nototheniidae. The distributions of these species with depth was similar to those described by Tiedtke and Kock (1989) for the fishes of Elephant Island.

Champsocephalus gunnari was the clear dominant both numerically and based on biomass (Fig. 2). One quarter of the biomass and nearly one third of the individuals were members of this species. It feeds almost strictly on krill (McKenna, 1991) and leads a more pelagic existance than the other icefish of the region (Kock, 1985b). *Notothenia gibberifrons* was a close second in biomass and was the third most abundant species. It is adapted to an epibenthic environ-

Table 1

Species codes and rareness designations. R = RARE (occurred at 5% or fewer of the stations sampled). U = UNCOMMON (occurred at 25% or fewer of the stations sampled). C = COMMON (occurred at more than 25% of the stations sampled). '—' indicates that that species was not caught during a particular survey.

Species code	Family and species	Rareness designation 86–87	87–88	88–89
	Artedidraconidae (Plunderfishes)			
ARTE	*Artididraco mirus*	C	C	C
	Bathydraconidae (Dragonfishes)			
BATH	*Bathydraconidae* spp.	R	—	—
PARA	*Parachaenichthys georgianus*	C	C	C
PSIL	*Psilodraco breviceps*	U	U	U
	Bothidae (Armless Flounders)			
MANT	*Mancopsetta maculata*	U	U	R
	Centrolophidae (Ruffs)			
CENT	*Centrolophidae* spp.	—	R	—
	Channichthyidae (Icefishes)			
ACER	*Chaenocephalus aceratus*	C	C	C
GUNN	*Champsocephalus gunnari*	C	C	C
PSEU	*Pseudochaenichthys georgianus*	C	C	C
	Gempylidae (Snake Mackerels)			
DIPL	*Paradiplospinus antarcticusa*		R	—
	Harpagiferidae (Spiny Plunderfishes)			
HARP	*Harpagifer georgianus*	—	R	—
	Liparididae (Snailfishes)			
CARE	*Careproctus georgianus*	—	R	—
LIPA	*Paraliparis* spp.	U	U	U
	Muraenolepididae (Moray Cods)			
MICR	*Muraenolepis microps*	C	C	C
	Myctophidae (Lanternfishes)			
ELEC	*Electrona antarctica*	R	—	R
MYCT	*Myctophidae* spp.	U	—	—
NICH	*Gymnoscopelus nicholsi*	U	R	—
	Nototheniidae (Antarctic Rock Cods)			
ANGU	*Notothenia angustifrons*	R	R	R
ELEG	*Dissostichus eleginoides*	C	C	R
GIBB	*Notothenia gibberifrons*	C	C	C
GUNT	*Patagonothen brevicauda*	R	R	—
HANS	*Pagothenia hansoni*	C	C	U
KEMP	*Notothenia kempi*	R	R	—
LARS	*Nototheniops larseni*	C	C	C
NUDI	*Nototheniops nudifrons*	C	C	C
ROSS	*Notothenia rossii*	C	C	U
SQUA	*Notothenia squamifrons*	C	U	-
	Rajidae (Skates)			
RAJA	*Raja georgiana*	C	U	U
	Zoarcidae (Eelpouts)			
MELA	*Melanostigma gelatinosum*		R	—

ment (Daniels, 1982) and feeds on invertebrate infauna, primarily polychete worms (McKenna, 1991). *Nototheniops larseni* was the second most abundant species and is the most pelagically adapted of the common species (Targett, 1981). It is a relatively small fish (<25 cm) that feeds on krill and other pelagic invertebrates (McKenna, 1991). *Chaenocephalus aceratus* and *P. georgianus* are the other two icefish found in the vacinity of South Georgia Island. Both species are closely associated with the sea floor and feed heavily on other fish and krill (McKenna, 1991). *Notothenia squamifrons* is a demersal rock cod that prefers the deeper strata of the region. It feeds on a wide variety of benthic invertebrates but has a preference for tunicates (McKenna, 1991). *Nototheniops nudifrons* is one of the smallest species in the region (10-5 cm). It lives in and among the sedentary megainvertebrates growing on the bottom (e.g., sponges). It feeds on benthic epifauna, but most of its diet consists of krill (McKenna, 1991). Other species collected by the AMLR surveys generally accounted for less than 2% of the fish in the region. For a more detailed description of this community see Gabriel (1987), McKenna and Saila (1989, 1991), and McKenna (1991).

Diversity values were moderate throughout the region and relatively consistent from year to year. The overall diversities (H') for each survey (1986–87–1988–89) were 1.51, 1.94, and 1.83 (based on numerical abundances) (Table 2). The value for any given station ranged from 0 to 2.097 (Fig. 3). Richness never exceeded 16 at a single station, but was as low as 1 (which accounts for the zero H' values) in a few cases. Survey-wide richness was nearly the same for 1986–87 and 1987–88 but declined in 1988–89 because of the lack of rare species collected during the survey. Overall evenness for each survey ranged from 1.02 to 1.35 and was greater in the latter two surveys.

Significant associations were found between species within each survey. However, all were weakly correlated (Table 3). Only three associations had r' values greater than 60% and none explained more than 70% of the variability in their distributions. None of the fifteen associations with r' values greater than 50% were consistent from year to year. However, three of these associations (*C. aceratus-P. georgianus*, *Artedidraco mirus-N. nudifrons*, *Muraenolepis microps-N. nudifrons*) persisted from 1986–87 to 1987–88. The inverse (Q-mode) cluster analysis appeared to classify the species into groups based on their relative rareness, but there were exceptions to such a classification in nearly every group.

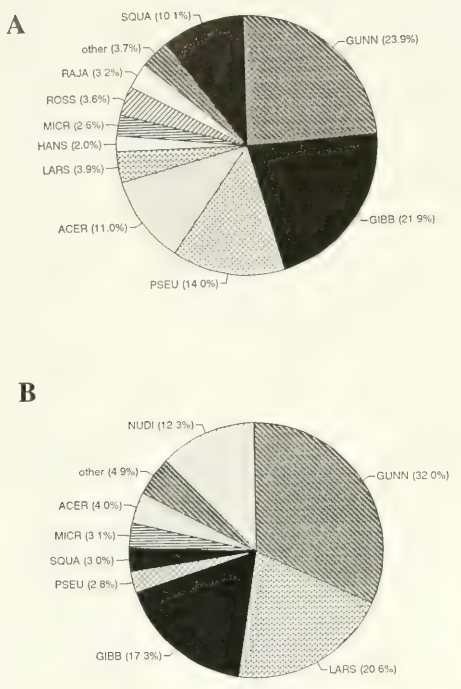

Figure 2

Pie charts illustrating the average composition of the demersal fish community around South Georgia Island during the AMLR surveys. (**A**) Composition based on the biomasses of the fish collected; (**B**) composition based on the numerical abundance of the fish collected.

Table 2

Diversity of South Georgia Island Demersal Fish Community. R represents species richness. The # symbol indicates that the diversity values were calculated on a numerical abundance basis. The wt. symbol indicates that the diversity values were calculated on a biomass basis. H' is the Shannon-Wiener information index. V is an index of species evenness.

	1986–87		1987–88		1988–89	
	R=27		R=25		R=18	
	#	wt.	#	wt.	#	wt.
H	1.51	1.91	1.94	1.94	1.83	1.99
V	1.02	1.29	1.31	1.31	1.24	1.35

The distribution of species abundances at most stations was described well by the logarithmic series model (Fig. 4). However, 27% of the stations (11) in the 1988–89 biomass data set fit the logarithmic series model poorly, while those of earlier surveys had less than half that proportion of poor fitting stations. The biomass data sets generally had more poor fitting stations than did the numerical data sets.

The normal cluster analyses clearly demonstrated that there was little spatial structure in the demersal fish community. Extensive chaining (Boesch, 1977; Jain and Dubes, 1988), frequent reversals (crossovers) (Kobayashi, 1987), and low number of significant clusters were indicative of the absence of spatial structure (Fig. 5, page 484). The 1986–87 and 1987–88 communities displayed slightly more significant structure than that in 1988–89, but chaining and reversals were prevalent there as well. The nodal analyses demonstrated that the species groups occurred with similar constancy throughout the region and fidelity was not strong for any particular group (Fig. 6, page 484).

Species composition of significant clusters was basically the same as that for the region-wide species assemblage (Fig. 2), except for those clusters formed by a small number of samples with rare species (Fig. 7, page 485). Clusters containing samples from Shag Rocks had *Patagonothen brevicauda* as an additional component. Close examination of the clusterings revealed that the presence or absence of the rarest species was the basis for what little structure was present. When these rare species (those which occurred at 5% or fewer stations) were removed, all or nearly all significant structure disappeared. The lack of structure was consistent from year to year.

Clustering of the length distribution of each species revealed little structure there as well. *Notothenia gibberifrons, C. gunnari,* and *N. larseni* showed a weak separation of large and small fish; large fish associated with deeper water and small fish with shallower stations during 1987–88 (Figures 8, A and B; 9A). Only *N. larseni* continued to show that trend in 1988–89 (Fig. 9B). *Notothenia larseni* also displayed a temporal separation in size, with larger fish caught later in the cruise in both surveys (Fig. 9C). *Muraenolepis microps* showed a similar weak trend of larger fish later in the cruise during the 1988–89 survey (Fig. 8C).

The gradient analyses revealed several significant, but weak trends. Skewer analysis detected significant trends in longitude in all three years. Significant trends in latitude and depth were identified in 1987–88 and in 1988–89. In 1986–87 and 1988–89, significant tem-

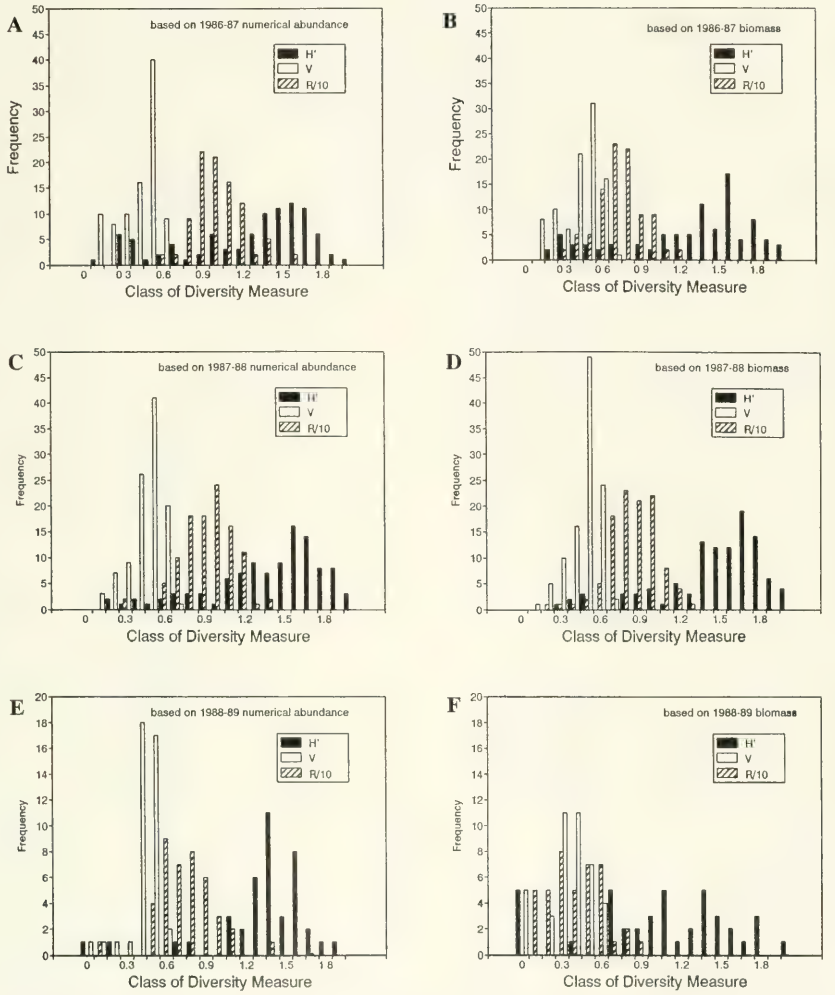

Figure 3

Distributions of diversity values for each AMLR survey. H' (SOLID BAR) represents the Shannon-Wiener Diversity index, and V (OPEN BAR) represents evenness, R (SHADED BAR) represents richness. (Richness was adjusted to the scale of the other indices by dividing by 10.) (**A**) Diversity of fish community at stations sampled during the 1986–87 survey, based on numerical abundance; (**B**) diversity of fish community at stations sampled during the 1986–87 survey, based on biomass; (**C**) diversity of fish community at stations sampled during the 1987–88 survey, based on numerical abundance; (**D**) diversity of fish community at stations sampled during the 1987–88 survey, based on biomass; (**E**) diversity of fish community at stations sampled during the 1988–89 survey, based on numerical abundance; (**F**) diversity of fish community at stations sampled during the 1988–89 survey, based on biomass.

Table 3

Results of spearman rank correlation analyses on common Antarctic demersal fish species associations. All correlation values in this table were significant at the 0.01 level when tested against the null hypothesis of zero correlation.

1986/87		1987/88		1988/89	
Species pair	r'	Species pair	r'	Species pair	r'
ACER-ARTE	–0.40	ACER-GUNN	+0.30	GIBB-LARS	+0.50
ACER-GIBB	+0.35	ACER-PSEU	+0.55	GIBB-MICR	+0.51
ACER-GUNN	+0.31	ACER-PSIL	+0.29	LARS-ACER	+0.54
ACER-NUDI	–0.33	ACER-RAJA	+0.33	LARS-MICR	+0.59
ACER-PSEU	+0.52	ARTE-ELEG	–0.38	MICR-ACER	+0.48
ARTE-MICR	–0.64	ARTE-GIBB	+0.26		
ARTE-NUDI	+0.70	ARTE-HANS	–0.39		
ARTE-PARA	+0.36	ARTE-MICR	–0.40		
ARTE-PSEU	–0.47	ARTE-NUDI	+0.60		
ARTE-RAJA	+0.35	ELEG-HANS	+0.40		
ARTE-SQUA	–0.49	ELEG-MANT	+0.43		
ELEG-ARTE	–0.36	ELEG-NUDI	–0.38		
ELEG-HANS	–0.47	GIBB-LARS	+0.28		
ELEG-NUDI	–0.37	GIBB-NUDI	+0.36		
ELEG-PSEU	–0.36	GIBB-PARA	+0.30		
ELEG-ROSS	–0.46	GIBB-PSIL	+0.26		
GIBB-LARS	+0.29	GIBB-ROSS	+0.34		
GIBB-NUDI	+0.33	GUNN-PSEU	+0.40		
GIBB-PARA	+0.30	GUNN-PSIL	+0.33		
GIBB-PSEU	+0.32	HANS-NUDI	–0.36		
GIBB-PSIL	+0.41	HANS-PSEU	+0.28		
GIBB-ROSS	+0.36	LARS-PARA	+0.30		
GUNN-PARA	+0.34	LARS-PSIL	+0.41		
GUNN-PSEU	+0.34	LARS-RAJA	+0.40		
HANS-PSIL	+0.36	MICR-MANT	+0.34		
LARS-PARA	+0.46	MICR-NUDI	–0.55		
LARS-PSIL	+0.36	MICR-PARA	–0.32		
MICR-MANT	+0.56	MICR-PSIL	+0.31		
MICR-NUDI	–0.63	MICR-RAJA	+0.35		
MICR-PARA	–0.39	PSEU-PSIL	+0.35		
MICR-SQUA	+0.59				
NUDI-RAJA	–0.29				
NUDI-SQUA	–0.37				
PARA-LARS	+0.46				
PARA-NUDI	+0.49				
PARA-SQUA	+0.35				
PSEU-NUDI	–0.41				
SQUA-MANT	+0.53				
SQUA-RAJA	–0.40				

poral trends also existed. However, all of the trends revealed by skewer analysis were weak; the primary mode fell into either the smallest or second smallest class interval of Tau (Fig. 10, page 487).

Gradient analysis, using GRADSECT.BAS, measures the rate of change of the species assemblage along the gradient of interest. However, it offers no objective decision about the value that the rate must reach in order to be considered significant. Thus, it will identify ecotones along any gradient and it is a matter of subjective judgment to determine which (if any) of the peaks are real boundaries between communities (Fig. 11, page 488). Figure 12, page 488 summarizes the most pronounced boundaries from each of the gradients examined.

Discussion

The diversity values for the South Georgian fish community were generally greater than those reported by Targett (1981) for the same region. They were within the range of those reported for demersal fish in tropical estuarine areas (Yanez-Arancibia et al., 1980). These values place the South Georgia fish community on the relative, global diversity continuum, but the wide range of values demonstrates that diversity alone is a poor model of this community.

The richness component of diversity was low and similar to that reported by Targett (1981), but the evenness was considerably larger than had been reported for this region. This observation is consistent with the finding that a significant shift in the species assemblage from 1986–87 to 1987–88 was associated with an increase in diversity because of an increase in the evenness component of that index (McKenna and Saila, 1991). The increasing number of stations that poorly fit the logarithmic series distribution with time also supports the hypothesis that the community was changing toward one which was less dominated by a small number of species. This apparent change in the community was compounded in 1988–89 by the use of different sampling techniques and gear. The sampling during that season was insufficient to accurately represent the abundance of the rarest species. A bias was also introduced by the small gear used for that survey. In all previous AMLR surveys the mackerel icefish (*C. gunnari*) was the most abundant species. The smaller individuals of this species tends to be more pelagic than many of the others

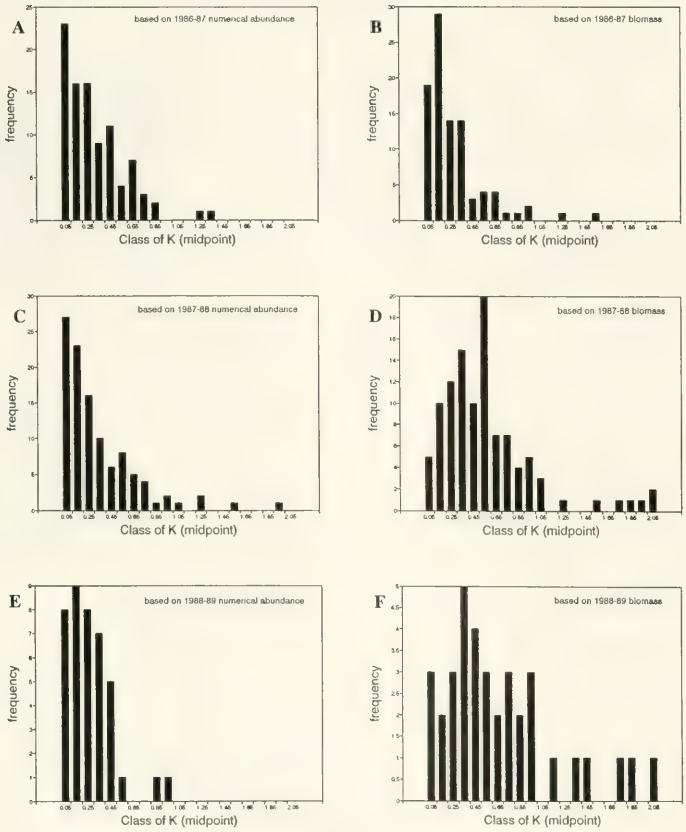

Figure 4

Distributions of *K*-values from fit to the logarithmic series distribution for each AMLR survey. *K* values >2 are not shown. (**A**) *K*-values of fish community at stations sampled during the 1986–87 survey, based on numerical abundance; (**B**) *K*-values of fish community at stations sampled during the 1986–87 survey, based on biomass; (**C**) *K*-values of fish community at stations sampled during the 1987–88 survey, based on numerical abundance; (**D**) *K*-values of fish community at stations sampled during the 1987–88 survey, based on biomass; (**E**) *K*-values of fish community at stations sampled during the 1988–89 survey, based on numerical abundance; (**F**) *K*-values of fish community at stations sampled during the 1988–89 survey, based on biomass.

in this system (Slosarczyk, 1983). The smaller gear might have missed some concentrations of this species, thus underestimating its population and diminishing the apparent dominance of the community.

The species associations and distribution of species groups were weak and inconsistent. The association between *A. mirus* and *N. nudifrons* was the strongest and still only accounted for, at most, 70% of the variability in their distributions (Table 3). Both of these fish are small (<15 cm), benthic species; however, their diets overlapped only slightly (38%) (McKenna, 1991). They were often removed from within sponges and other large invertebrates that formed a major part of the catch. They were not numerically dominant, but they were ubiquitous in the region. Although their distributions may have been linked, the association is probably more indicative of how widespread their preferred habitat is (i.e. habitat containing an abundance

Figure 5

Results of cluster analysis of the 1988–89 AMLR survey data. Station labels are read vertically under each branch of the dendrogram. The dashed line represents the level at which significantly different clusters begin. (**A**) Dendrogram of clustering based on numerical abundance; (**B**) dendrogram of clustering based on biomass.

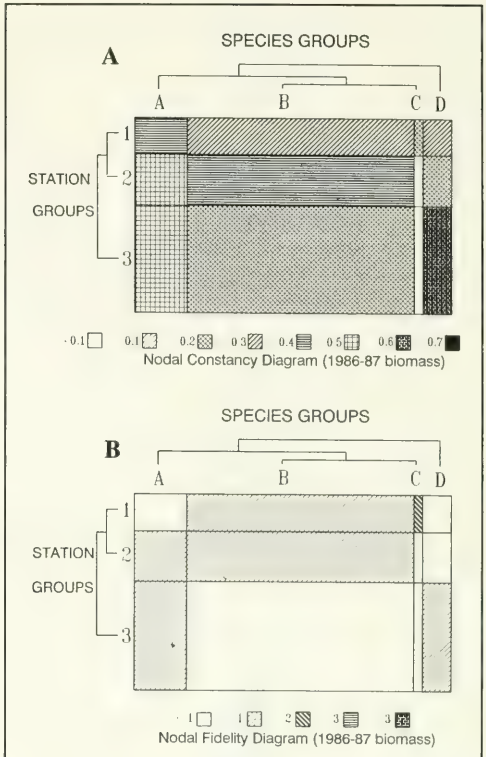

Figure 6

Results of nodal analysis of the 1986–87 AMLR survey data, based on biomass. The width of each band is proportional to the number of entities in the associated group.

of large, epibenthic invertebrates: branching sponges, corals, tunicates, crinoides, etc.).

The *C. aceratus-P. georgianus* association is most likely a result of the similar feeding behavior and habitat preferences of these species. Both are relatively sedentary, benthic fish which feed heavily on krill and other fish. Their diets strongly overlap (64%, McKenna, 1991) and their distribution may well reflect the distribution of their prey.

Significant associations suggest some biological interactions between the species involved. However, little can be said about the cause of these associations. Two species may display a negative association owing to distinct habitat requirements; they may have similar habitat requirements but experience a niche shift because of competition (McNaughton and Wolf, 1979b); or they may not coexist because of predation by one on the other. Most of the significant negative associations in this study involved one piscivorous member (McKenna, 1991), which suggests predator-prey relationships. The strongest of these negative associations were between *M. microps* and two of the smallest species in the region, *N. nudifrons* and *A. mirus* (Table 3). These three species are found close to the bottom and much of their diet consists of benthic organisms (37% overlap, McKenna, 1991). However, *M. microps* grows to over twice the size of the other two (Fischer and Hureau, 1985) and will feed on fish (McKenna, 1991) (though its small mouth probably limits any predation on the other two species to juveniles). Information about available habitats and the diets of the individuals within each habitat are necessary before these relationships may be more clearly defined for the South Georgia system.

The classification of the species into groups (by inverse clustering) and their distributions were not

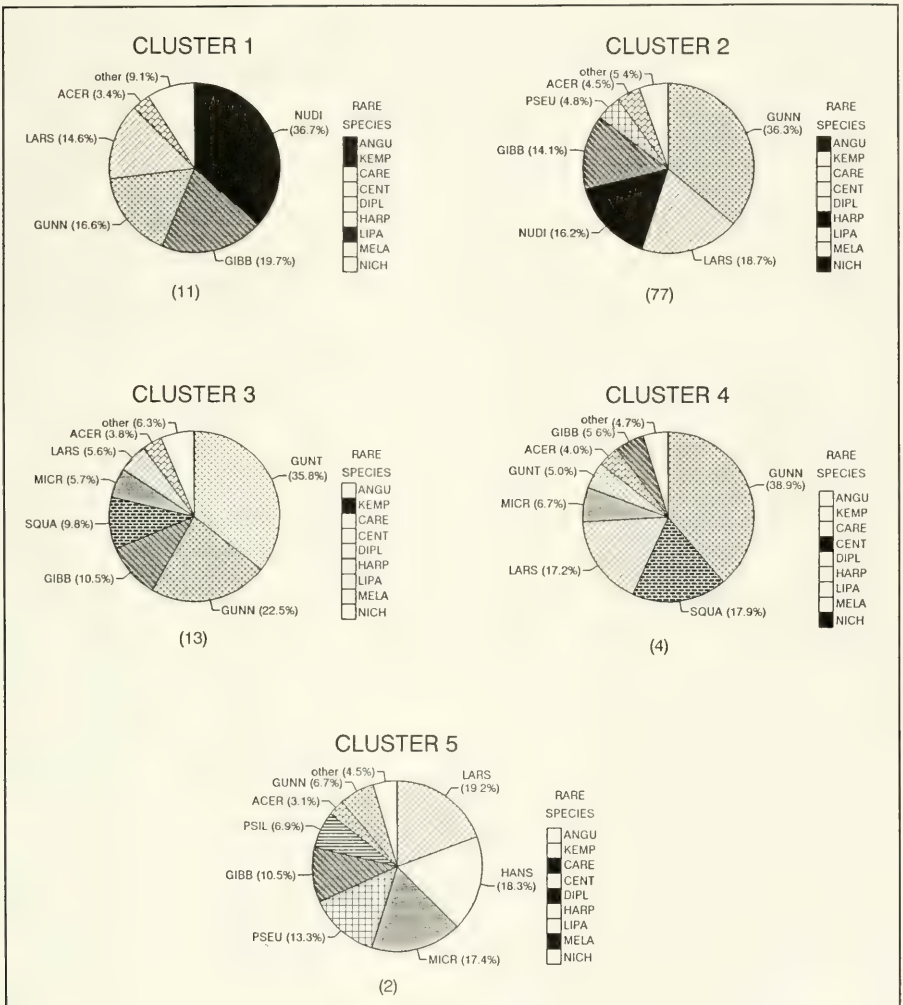

Figure 7

Charts describing the composition of the communities identified by cluster analysis of the 1987–88 AMLR survey data, based on numerical abundance. Pie charts depicting the composition of each community. Stations comprising each cluster are listed horizontally below each chart. The species which accounted for at least 10% of the community are listed to the left of each chart. Bars depicting the presence/absence of the rarest species in each community. Shaded boxes indicate presence. Stations comprising each cluster are listed horizontally below each chart. Species codes are read vertically under each box of a given bar.

clearly defined. The weakness of the pairwise associations and the nebulous basis for the classification of species into groups suggests the lack of stronger ecological ties between some species than others in the community.

Normal (*R*-mode) clustering of sample sites based on both species assemblages and size structure of each species' population indicated the lack of spatial structure in the community, as well. The movement of fish towards deeper water as they grow larger offers a pos-

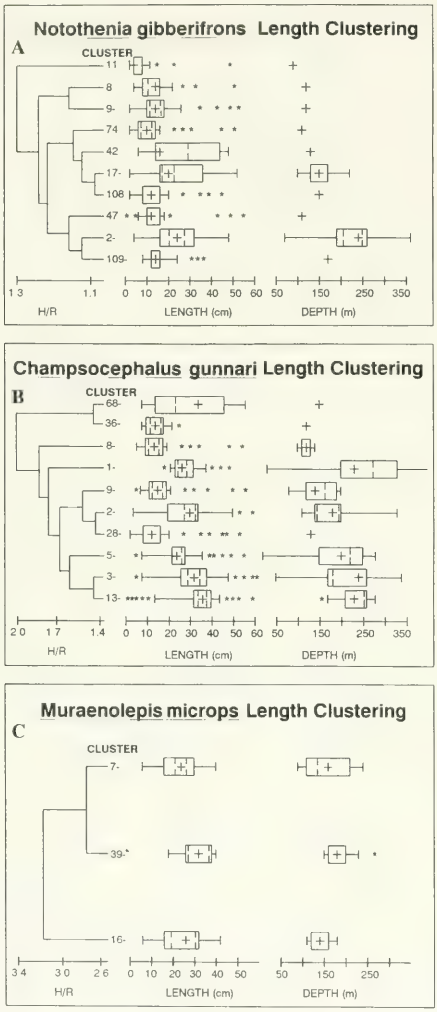

Figure 8

Results of cluster analysis of the size structure of three fish populations around South Georgia Island. Each dendrogram depicts the classification of samples according to the size composition of the associated fish population. Box plots describe the location and spread of the total length of fish in each cluster and the depth or sequential order of the stations that comprise each cluster. The broken verticle lines within each box represent the upper and lower notches and provide a rough measure of the significance of differences between medians (Hoaglin et al., 1983). **A** = *N. gibberifrons* during 1987–88 survey compared with depth; **B** = *C. gunnari* during 1987–88 survey compared with depth; **C** = *M. microps* during 1988–89 survey compared with sample order.

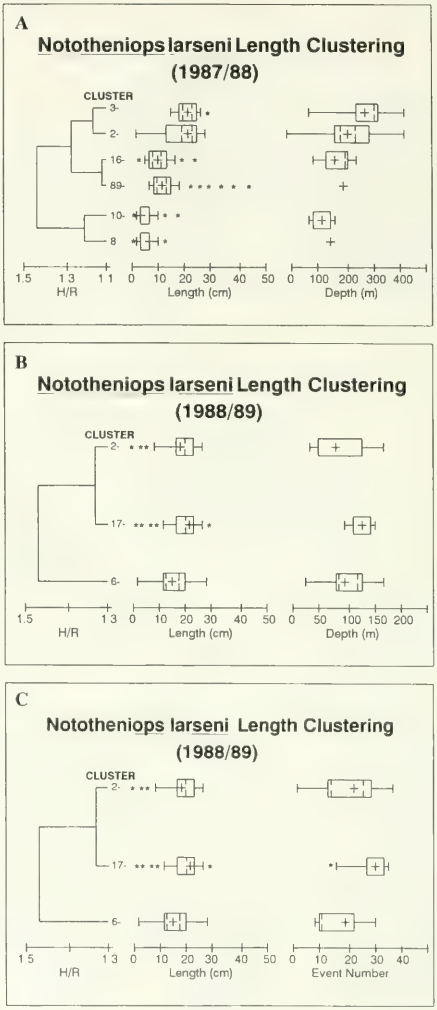

Figure 9

Results of cluster analysis of the size structure of the *N. larseni* fish population around South Georgia Island. Each dendrogram depicts the classification of samples according to the size composition of the associated fish population. Box plots describe the location and spread of the total length of fish in each cluster and the depth or sequential order of the stations that comprise each cluster. The broken verticle lines within each box represent the upper and lower notches and provide a rough measure of the significance of differences between medians (Hoaglin et al., 1983). **A** = Comparison of 1987–88 population with depth; **B** = comparison of 1988–89 population with depth; **C** = comparison of 1988–89 population with sample order.

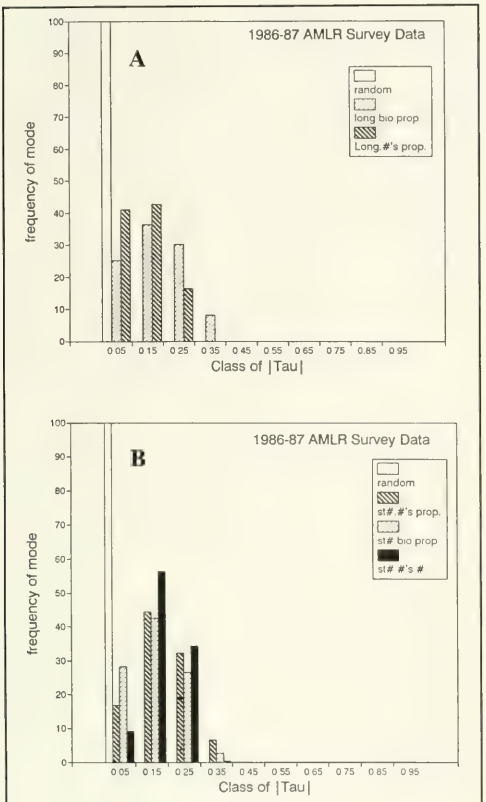

Figure 10

Results of skewer analysis of the 1986–87 AMLR survey data. LEGEND: random indicates the bar representing the results from the 20 random tables generated by each analysis. long. = longitude; st# = station number; # = analysis based on numerical abundance; bio. = analysis based on biomass; prop. = use of proportion. (**A**) Histogram indicating the frequency of the location of the primary mode while examining the trend in longitude; (**B**) histogram indicating the frequency of the location of the primary mode while examining the trend in date (as indicated by station number).

sible explanation for changes in size structure of some of the species within a survey. However, those trends were all weak and inconsistent. In general the results indicate that there was little or no structure to the demersal fish community of South Georgia Island. No areas that could be considered nurseries were identified. Nor were there areas of particularly high abundance of only the most valuable commercial species. Variability in the abundance of each species was evident. However, essentially the same assemblage with similar dominant species was found at nearly every sampled location on the continental shelf. This consistency in the species assemblage has been noted in the South Georgia region before (Targett, 1981).

The absence of spatial structure is unusual in natural communities and it is unclear why this situation exists in the South Georgia Island system. The species within this community can be classified into three trophic groups: krill-eaters (e.g., *C. gunnari* and *N. larseni*), piscivores (e.g., C. *aceratus* and *P. georgianus*), and benthic invertebrate feeders (e.g., *N. gibberfrons* and *N. squamifrons*) (McKenna, 1991). One would expect these animals to be distributed according to the availability of their prey or appropriate habitat (or both). Although the trophic groups are clear, they are closely linked and the distribution of all these species may be dependent on the abundance and distribution of krill (*Euphausia superba*). If krill was superabundant then, even if it were patchy, it might have more than met the demands of the krill-eaters, explaining their uniform distribution. The piscivores will follow their fish prey, which fed either on krill or some benthic resource. The benthic invertebrate feeders were also uniformly distributed. Little is known about the benthic community around South Georgia Island. However, it has been shown that most of the organisms of that habitat are inedible to fish (Belyaev and Ushakov, 1957). It might be expected then that the edible benthic resources are distributed in patches within this habitat. That was not apparent from the distribution of the fish and may have been concealed by the fact that even the benthic feeders ate krill (McKenna, 1991), including *N. gibberifrons* and *N. nudifrons*. These two species are highly adapted to feeding on benthic organisms and yet their diets included krill. Targett (1981) also observed krill in the diet of these benthic-feeding species and suggested that a shoal of krill had moved into shallow water and was forced close to, or in actual contact with, the bottom. This would seem to be an indication of the great abundance of krill in the vicinity of South Georgia Island.

The results of this research imply that during the austral summer there was, in general, a uniform distribution of the necessary resources throughout the sampled region, at scales of 10 km to 100's of km. It must be emphasized that these surveys took place only in the summer and little is known about this community at other times of the year. The strong seasonality of this environment may present the inhabitants with an annual 'boom' and 'bust' cycle, having abundant resources in the summer and a 'bottleneck' period (when resources are less available than at other time of year) during the winter (Wiens, 1977; DuBowy, 1988). The abundance of available resources during the summer may allow different species to feed on the same

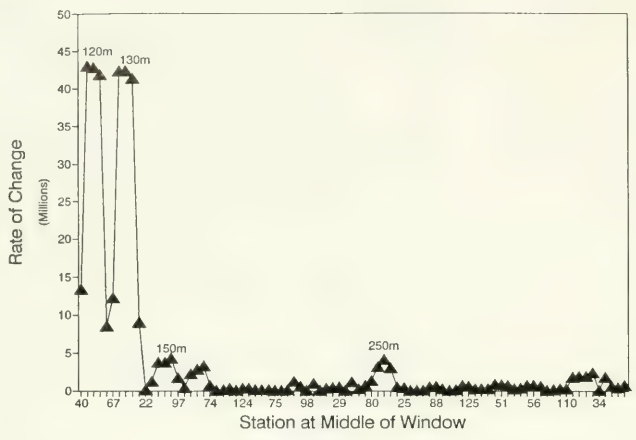

Figure 11
Example output from gradient analysis performed by GRADSECT, with the 1986–87 AMLR survey data sorted by depth.

resource (e.g., krill) without experiencing competition (McKenna, 1991). However, during the long winter, resources may be limiting, causing strict resource partitioning, and more highly defined community structure may develop. If this is the case, the events of the austral winter will be more important to regulation of the populations of these species than will those of the summer. To better understand this ecosystem, information on the seasonal dynamics of the community and its constituent populations (including krill and benthic invertebrates) is needed.

Acknowledgments

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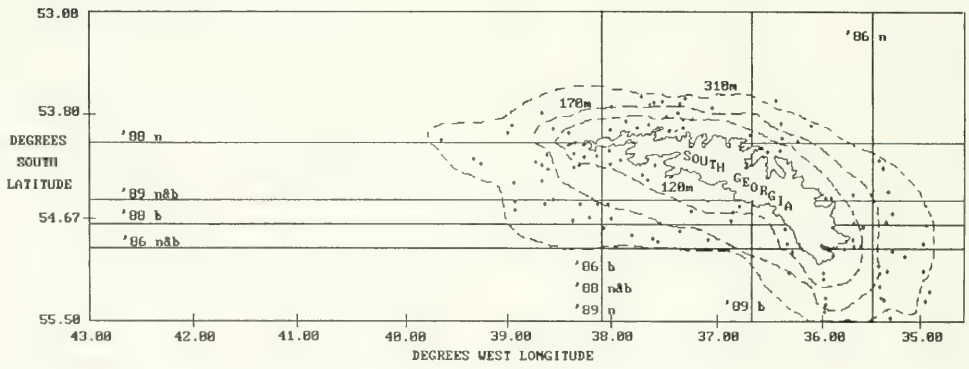

Figure 12
Summary of major ecotones identified by GRADSECT analysis. The horizontal lines represent the location of major breaks in the latitudinal gradient. The vertical lines represent the location of major breaks in the longitudinal gradient. The dashed lines represent the major breaks identified along the depth gradient. Abbreviations: '86 = based on 1986–87 survey data; '88 = based on 1988–89 survey data; n = based on numerical abundance; b = based on biomass.

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Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia

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Abstract.–A bioenergetic population model that integrated input on the abundance, distribution, sex- and age-structure, feeding rates, and diet of harbor seals was developed and used to estimate annual prey consumption in the Strait of Georgia during 1988. Owing to recruitment and mortality, the size of the Strait of Georgia population fluctuated seasonally from a minimum of 12,990 prior to the pupping season to a maximum of 15,810 following pupping. The study population represented a population that was increasing at an intrinsic rate of 12.5% per annum and was therefore skewed toward younger age-classes. Mean daily *per capita* gross energy requirements were estimated at 172 watts, of which 30% was lost in faeces, urine, and the heat increment associated with feeding, 42.3% was expended for basal metabolism, 23.4% for activity, 1.2% for body growth, and 3.2% for reproduction. Mean daily *per capita* food requirements were estimated to be 1.9 kg, or 4.3% of mean body mass. Diet composition varied seasonally: hake was dominant during April–November and herring during December–March. Combined, hake and herring accounted for 75% of the diet both in terms of energy and biomass. Total annual consumption was estimated at 9,892 (range 6,432–13,359) metric tons, which comprised 4,214 (2,215–6,664) t of hake, 3,206 (1,679–5,818) t of herring, 398 (171–846) tons of salmon, 335 (135–745) t of plainfin midshipman, 294 (137–556) t of lingcod, and the remaining 1,445 t of a wide variety of different prey. Gross and net population efficiency was estimated to be 3.9% and 2.2% in terms of energy, and 1.6% and 0.9% in terms of biomass.

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Fishery Bulletin 91:491–515 (1993).

The recovery of many formerly depleted pinniped populations and the rapid expansion of fisheries has prompted concern over potential pinniped-fishery conflicts (Mate[1]; Beverton, 1982; Contos[2]; Melteff and Rosenberg, 1984; Beddington et al., 1985; Harwood and Croxall, 1988). The nature of these conflicts can be broadly categorized as operational (direct) or as ecological (indirect) interactions (e.g., Mate and Harvey, 1987). Operational interactions encompass those that occur when pinnipeds and fishing operations come in direct contact. For example, pinnipeds may be injured or killed in fishing gear, and fishing gear and catches may be damaged by pinnipeds (Beach et al.[3]; DeMaster et al., 1982; Mate and Harvey, 1987). Since these interactions can be observed, they are relatively straightforward, at least conceptually, to assess through observer programs, logbooks, or interview surveys.

Ecological interactions, in contrast, encompass the indirect effects of pinnipeds on fisheries and fisheries on pinnipeds. For example, sustainable harvest levels may be reduced as a result of pinniped predation on valuable prey species, and the carrying capacity of pinniped populations may be reduced by human exploitation of their prey. Because these interactions are temporally or spatially displaced, or both, they are conceptually more difficult to assess than operational interactions. In their comprehensive review, Lavigne et al. (1982) outlined how the prey requirements of pinnipeds could be addressed using a bioenergetics approach, and how the approach could be extended to the population level. However, such population assessments require detailed information on the abundance, distribution, sex- and age-structure, feeding rates, and diet of pinnipeds, as well as the interactions between these variables. For example, feeding rates (in biomass) are dependent upon the quality of the diet, and vary both with the sex and age of animals. The distribution and diet of pinnipeds may also be correlated if their seasonal movements are dictated by changes in the local and seasonal abundance of their prey.

In British Columbia, recent concern over potential pinniped—fishery conflicts has focused mainly on the harbor seal (*Phoca vitulina*) (Malouf, 1986). Historic and recent manage-

[1]Mate, B. R. 1980. Workshop on marine mammal fisheries interactions. U.S. Dep. Commer. Rep. PBH80-175144, 48 p.

[2]Contos, S. M. 1982. Workshop on marine mammal-fisheries interactions. Final report for MMC contract MM2079341-0. NTIS PB82-189507, 64 p.

[3]Beach, R. J., A. C. Geiger, S. J. Jefferies, and S. D. Treacy. 1982. Marine mammal fisheries interactions in the Columbia River and adjacent waters. 2nd Annual Rep., Nov. 1, 1980–Nov. 1, 1981. Natl. Marine Mammal Lab., NWAFC Proc. Rep. 82–04, 186 p.

ment issues concerning harbor seals in British Columbia are similar to those facing pinnipeds in other regions. Earlier this century (1913–64), harbor seal populations throughout the province were maintained below historic levels by government-sponsored predator control hunts and bounty kills (Fisher, 1952; Bigg, 1969). During 1963–68, populations were further depleted by an intense commercial harvest for pelts[4]. However, in 1970 the species was protected and since then harbor seal populations throughout British Columbia have been increasing exponentially at an annual finite rate of about 12.5% (Olesiuk et al., 1990a). Abundance in British Columbia is estimated to have increased from 9,000–10,500 in 1970 to 75,000–88,000 by 1988 (Olesiuk et al., 1990a).

Investigations of harbor seals in British Columbia, particularly the Strait of Georgia, have provided much of the background information necessary to assess predator-prey interactions. Bigg (1969) described life history and population parameters, which were recently combined with information on the status of the population to construct life tables and a population model[4]. Aerial harbor seal censuses have been conducted in the Strait of Georgia periodically since 1966 and annually since 1982 to determine abundance and monitor population trends (Olesiuk et al., 1990a). Olesiuk et al. (1990b) recently described regional and seasonal variations in diet composition based on scat analyses. In addition to these local studies, the energetics of captive harbor seals and related phocids has been investigated in some detail by other researchers, and feeding rates of free-ranging harbor seals have been estimated from the volume of prey in stomachs collected on the east coast of Canada (Boulva and McLaren, 1979).

In this report, I synthesize these data into a bioenergetic population model and use the model to estimate annual prey consumption by harbor seals in the Strait of Georgia. The model serves several purposes. First, it provides improved estimates of the annual consumption by harbor seals of commercially and recreationally utilized species, which may be of particular interest to resource managers who must base real-time management decisions on the best information currently available. Second, the model identifies the relative sensitivity of the prey consumption estimates to, and the present level of certainty in, each of its parameters, and is therefore useful for directing future research. Third, the model provides a framework for examining interactions between its individual components. For example, Olesiuk[4] employed the model to predict the effects of demographic changes in harbor seal populations on mean *per capita* energy requirements. Finally, the basic model serves as a foundation upon which additional refinements can be added as more accurate and detailed information becomes available. For example, the basic model is a prerequisite for more elaborate models that incorporate the depensatory and compensatory responses of prey to their predators and predators to their prey (Beverton, 1985) or economic parameters (Clark, 1985).

Materials and methods

Study area

Annual prey consumption was estimated for harbor seals inhabiting the Strait of Georgia (Fig. 1) during the 1988 calendar year. The Strait of Georgia was selected for intensive study because the area is readily accessible and supports a higher concentration of harbor seals than other regions of British Columbia. Although the study area represents only 12% of the total British Columbia coastline, it supports 18–21% of the province's harbor seal population (Olesiuk et al., 1990a).

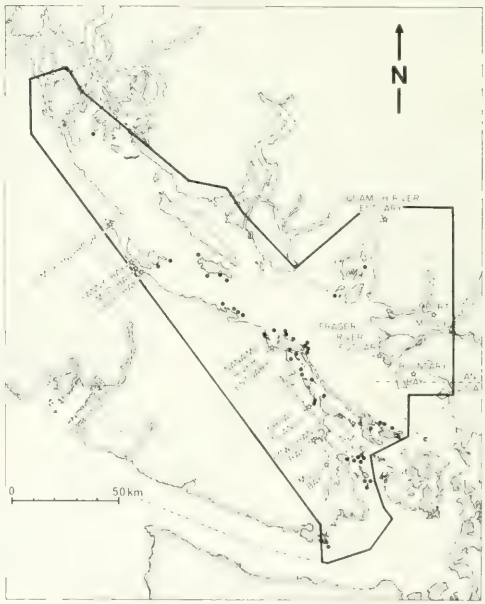

Figure 1
Map of southwestern British Columbia showing boundaries of the Strait of Georgia study area (solid line) and scat collection sites (○ = estuaries; ● = non-estuaries).

[4]Olesiuk, P. F. Population dynamics of the harbor seal (*Phoca vitulina*) in British Columbia. Manuscr. in prep.

The Strait of Georgia also supports important commercial and sport fisheries. With respect to salmon, the most valuable fishery, the study area accounts for approximately 28% by number and 31% by weight of total escapement in British Columbia[5]. Ketchen et al. (1983) estimated that the Strait of Georgia accounted for 27% of the total non-salmonid commercial harvest by weight, 34% by landed value, and 26% by wholesale value. The Strait of Georgia also accounts for about 96% of all recreational angler-days expended in the tidal waters of British Columbia (Sinclair[6]), which represents about 600,000 boat-trips annually (Shardlow and Collicutt, 1989). Harbor seal-fishery conflicts in the Strait of Georgia would therefore be expected to be more intense than in other regions of the province.

Two distinct types of habitat were recognized within the study area: estuaries and non-estuaries. Estuaries were defined as the large, shallow, soft-bottomed areas that occurred at the mouths of some rivers. Twelve estuaries (Fig. 1) within the study area were inhabited by appreciable numbers (≥10) of seals. In estuaries, seals typically hauled out on logbooms or on tidal sandbars. Seals were widely distributed outside of estuaries and utilized 285 different haulout sites, most of which consisted of tidal boulders, reefs, islets, and ledges at the base of bluffs (Olesiuk et al., 1990a).

The model

Input parameters for the model consisted of information on harbor seal abundance, distribution, the sex- and age-structure of the population, diet composition, and daily energy and food requirements. The first four parameters were derived from local studies (Bigg, 1969; Olesiuk et al., 1990a; Olesiuk et al., 1990b; Olesiuk[4]), whereas the last parameter was deduced from the metabolic and feeding rates reported for phocids in the literature. The primary output from the model consisted of estimates of the annual consumption of each prey species.

The annual consumption of a particular prey was estimated as the product of the abundance of seals, feeding rates, and the proportion of that prey in their overall diet. Daily food requirements were estimated separately for each sex-and age-class in the population, and mean *per capita* requirements calculated from energetic life tables by weighting the individual estimates according to the sex-and age-structure of the population. Feeding rates were assumed to be the same within and outside of estuaries and constant with season. However, because the abundance and diet composition of seals differed between estuaries and non-estuaries and varied seasonally in both habitat types (Olesiuk et al., 1990b), the abundance and diet data were stratified by habitat type and integrated over time. The biomass of the kth prey species consumed annually, B_k, was thus estimated as

$$B_k = \overline{FR} \cdot \int_1^{365} N_{Et} \cdot P_{Ekt} \cdot dt + \overline{FR} \cdot \int_1^{365} N_{0t} \cdot P_{0kt} \cdot dt \qquad [1]$$

where $\overline{FR}$ is the mean *per capita* daily food requirement, N_{Et} and N_{0t} the number of seals within and outside of estuaries, respectively, on the tth date (1=January 1st; 365=December 31st), and P_{Ekt} and P_{0kt} the proportion of the diet within and outside estuaries comprised of the kth prey species on the tth date. The integrals were solved by calculating finite approximations using daily Δt increments.

Abundance and distribution

The abundance and distribution of harbor seals in the study area were determined by aerial censuses. In 1988, the entire study area was surveyed twice; once just prior to the pupping season (31 May–16 June) and again at the end of the pupping season (9–26 August). A third estimate of the population size in 1988 was obtained by projecting the population trends observed during censuses conducted between 1973 and 1988.

Aerial censuses were conducted under standardized conditions under which maximum numbers of seals were hauled out: 1) the lower of semi-diurnal low tides; 2) between 08:00–11:30 AM; 3) usually toward the end of the pupping season which extends from early July to mid August (Bigg, 1969); and 4) not during inclement weather such as rough seas or heavy precipitation. Under these conditions, the variability of replicate censuses indicated that counts represented, on average, 88.4% of the actual population (Olesiuk et al., 1990a).

The confounding effects of seasonal fluctuations in the size of the population due to recruitment during the protracted pupping season were removed by adjusting all census counts, C_t, to post-pupping levels by applying a correction, P_t, to account for pups born subsequent to the date, t, of the census. Since births are normally distributed over time with a mean julian birth date, μ, of 208 (27 July) and σ of 16.1 days (Bigg, 1969; Olesiuk et al., 1990a), P_t was calculated as

$$P_t = 1 + \beta - \int_{-\infty}^{\frac{t-\mu}{\sigma}} 2\pi^{-0.5} \cdot e^{\frac{(t-\mu)^2}{2\sigma^2}} dt \cdot \beta \qquad [2]$$

[5]Estimated from data provided by G. Hudson, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1989.

[6]Sinclair, W. F. 1972. The British Columbia sport fisherman. Can. Dep. Environ. Fish. Serv., Pac. Reg., 69 p.

where β denotes the finite annual *per capita* birth rate (see Population Parameters).

The actual size of the population at the end of the pupping season, N_p, was thus estimated by correcting the original census counts, C_t, for both the estimated number of pups born subsequent to censuses and the mean proportion of seals missed during censuses:

$$N_p = C_t \cdot P_t \cdot 0.884^{-1} \quad [3]$$

Seasonal fluctuations in the size of the population due to recruitment during the pupping season and mortality throughout the year could not be directly monitored because low tides suitable for censuses occurred only at night prior to May and after October. Seasonal fluctuations were thus modeled by adjusting the post-pupping population estimate, N_p, for births and deaths. The Strait of Georgia population was assumed to be closed to immigration and emigration, which was realistic considering that harbor seals are non-migratory (Bigg, 1981) and that the density of seals in neighbouring areas are much lower than in the study area (Olesiuk et al., 1990a). The size of the population, N_t, on the tth date was thus estimated by

$$N_t = (N_p/P_t)e^{Z(t-p)} \quad [4]$$

where Z represents the instantaneous daily mortality rate. Assuming that mortality was uniformly distributed throughout the year, Z was obtained from the mean finite annual *per capita* mortality rate, ∂ (see Population Parameters):

$$Z = \{-\ln(1-\partial)\} \cdot 365^{-1} \quad [5]$$

Although it was not possible to monitor seasonal trends in abundance in the entire study area, seasonal trends in estuaries were monitored. Estuaries could be censused throughout the year because seals typically hauled out on logbooms that were exposed at all tides, and also because swimming seals could be counted in these shallow, confined areas. Between May 1988, and February 1989, a series of 5 aerial censuses of all estuaries, except Port Moody and the Squamish River estuary, were conducted at approximately 2-month intervals. The aerial counts were supplemented with periodic boat counts made during scat collections, and for Port Moody and the Squamish River estuary (which combined represented only 2–8% of the total number of seals in estuaries) with counts provided by knowledgeable volunteers. All counts for each estuary made in a particular month during 1988–89 were averaged and plotted at the mean date of the counts, and abundance linearly interpolated between consecutive estimates. The total number of seals outside estuaries on the tth date, N_{0t}, was subsequently estimated by subtracting the total count for all estuaries, N_{Et}, from the estimated total size of the population, N_t.

Population parameters

Population parameters were derived from a sample of 324 specimens collected by Bigg (1969) from the Strait of Georgia and neighbouring waters during 1964–69. The sample was collected following a long period (1913–64) over which the size of the harbor seal population had been reduced and maintained below natural levels by control kills and commercial harvests (Olesiuk[4]). Since the control and commercial kills were likely non-selective by sex or age, except for pups which were probably more vulnerable than older animals (Olesiuk[4]), Bigg's (1969) post-pup sample was considered to be representative of a population below carrying capacity with a stable sex- and age-structure. Since the study population has been increasing exponentially since 1970 (Olesiuk et al., 1990a), it has also likely attained a stable sex- and age-structure indicative of a population below carrying capacity.

Age-specific maturation rates were calculated from the data given in Bigg's (1969) Tables 1 and 2. Owing to the small sample size available for males, maturation rates of males were smoothed by calculating 3-point running means. Age-specific fecundity rates (i.e., the proportion of all females in an age-class that give birth each year), $FEC_{(x)}$, were calculated as the product of the age-specific pregnancy rates for mature females (Bigg, 1969; Olesiuk[4]) and the estimated proportion of females in each age-class that were mature.

The stable sex- and age-structure of the study population was estimated from the sex- and age-composition of a subsample of 245 animals aged ≥6.0 months that were considered to have been collected in a random fashion (Bigg, 1969). Following Bigg (1969), specimens aged 0–5.9 months were excluded from the analysis because of potential sampling biases, specimens aged 6.0–17.9 months were tallied as 1-year-olds, specimens aged 18.0–29.9 months as 2-year-olds, etc. The exponential rate of decline, r, in the relative number of animals of each sex, S (f=female and m=male) in age-classes, $N_{S(x)}$, with age, X, was smoothed by regressing the logarithm of the estimated number of survivors in each age-class on age, such that

$$N_{S(X+1)} = N_{S(X)} e^{-r_S} \quad [6]$$

The residuals from the log-linear regressions indicated that the rates of decline differed between sexes and

were not constant with age (Bigg, 1969; Olesiuk[4]). The best fitting series of log-linear segments was therefore obtained iteratively by applying piecewise regressions with varying inflection points. Because pups aged <6 months were likely over-represented in Bigg's (1969) sample, their abundance, $N_{s(0)}$, relative to older age-classes, $N_{s(x)}$, was calculated as

$$N_{s(0)} = 0.5 \cdot \sum_{X=1}^{MA_f} (N_{f,x} \cdot FEC_x), \quad [7]$$

which assumes that the sex ratio at birth was equal. The number of seals in each sex- and age-class at the end of the 1988 pupping was estimated by normalizing the relative $N_{s(x)}$ series to sum to N_p. Assuming that births occurred as a pulse at the beginning of the annual cycle and deaths throughout the year, the finite annual birth rate, β, was estimated as

$$\beta = (N_{f,0} + N_{m,0}) / (\sum_{X=1}^{MA_f} N_{f,x} + \sum_{X=1}^{MA_m} N_{m,x}), \quad [8]$$

and the mean annual finite death rate, ∂, as

$$\partial = 1 - (\alpha / [1+\beta]), \quad [9]$$

where α is the finite annual population multiplication rate (1.125; Olesiuk et al., 1990a) and MA_s denotes the maximum ages attained by each sex (see Results).

Rates of growth in body mass were calculated separately for each sex by fitting specialized von Bertalanffy curves (Zullinger et al., 1984) to the body mass at age data summarized in Bigg (1969). Ages were estimated to the nearest month by assuming that all animals were born in June. Owing to a small number of adult males in Bigg's (1969) sample, his data were supplemented with data for 10 males aged 10–25 years collected in the Gulf of Alaska (Bishop, 1967). Parameters of the specialized von Bertalanffy growth curves

$$M_{s,x} = A \cdot \{1 - 0.33 \cdot e^{-K \cdot X \cdot I}\}^3, \quad [10]$$

where $M_{s(x)}$ represents the body mass of sex S at age X, and A, K, and I are the growth parameters, were estimated iteratively by a Quasi-Newton method (Fletcher[7]) using least squares criteria.

Energetics

Daily food requirements were estimated from two sources of data: 1) energetic parameters reported in the literature for harbor seals and related phocids based on captive studies; and 2) volumes of undigested prey in the stomachs of harbor seals collected on the east coast of Canada (Boulva and McLaren, 1979). In both cases, daily food requirements were estimated separately for each sex- and age-class in the population based on their mean body masses, and mean *per capita* requirements calculated from energetic life tables by weighting the individual estimates according to the sex- and age-structure of the study population. Mean body masses of age-classes were obtained by taking the geometric mean of their estimated masses at the beginning and end of the age interval (Eqn. 10), which assumes that growth was uniform throughout the year. Energetic parameters were calculated according to the International System of Units (ASTM, 1982). Where necessary, non-conforming values in the literature were converted by assuming that 1 calorie = 4.184 joule (J), such that 1 kcal·day^{-1} = 0.0484 J·sec^{-1} or Watts (W). Where efficiency was not stated, net energy (NE) expenditures were transformed to gross energy (GE) requirements by assuming that overall efficiency was 70%; i.e. 13% of the GE in the diet, which usually consisted of herring, was not metabolizable (6% lost in feces and 7% in urine; Keiver et al., 1984) and 17% of GE was expended as the heat increment associated with feeding (Gallivan and Ronald, 1981).

The basal metabolic rates of adult pinnipeds (Lavigne et al., 1986), like those of other adult mammals, conform with Kleiber's (1975) relationship. The net basal metabolic rates of adults of aged X, $BMR_{s(x)}$ in watts, was therefore estimated as

$$BMR_{s,x} = 3.4 \cdot M_{s,x}^{0.75} \quad \text{(from Kleiber 1975)} \quad [11]$$

where $M_{s(x)}$ denotes the mean body mass (kg) of sex S at age X. Since other major components of the energetic budget also scale to $M^{0.75}$ (Lavigne, 1982), it is convenient to consider total energy requirements relative to BMR.

A large portion of the overall energy budget of seals is expended on maintenance, which encompasses the energy required for basal metabolism, activity and thermoregulation (Lavigne et al., 1982). Innes et al. (1987) provided one estimate of the gross maintenance requirements of non-growing, adult phocids based on the rates of energy ingestion in captivity, $MR1_{s(x)}$ in watts:

$$MR1_{s,x} = 7.5 \cdot M_{s(x)}^{0.71} \text{ (Eqn. 7 in Innes et. al. 1987)} \quad [12]$$

The metabolic rates of juveniles, however, are usually elevated relative to those of adults of equivalent mass (Innes et al., 1987). For mammals, the magnitude by which juvenile metabolic rates are elevated generally declines from a peak at the onset of feeding

[7]Fletcher, R. 1972. FORTRAN subroutines for minimization by quasi-Newton methods. AERER 7125.

to adult levels by the onset of maturity (Kleiber, 1975; Brody, 1945). Data given in Worthy (1987a)'s Figure 4, together with his reported efficiency of 68%, indicates that the gross maintenance requirements of neonate harp and grey seals increases to about 1.8× the predicted adult $MR1$ (Eqn. 12) at the onset of feeding. In the absence of precise empirical data on the ontogeny of juvenile harbor seal metabolic rates, it was assumed that $MR1$ converged from a post-weaning maximum of 1.8× the predicted adult $MR1$ at the onset of feeding to adult $MR1$ levels at the onset of sexual maturity in an exponential fashion. A multiplier to account for elevated metabolic rates of juveniles at a given age, $JCF_{s(x)}$, was thus derived by calculating a series of 3- 4- 5- and 6-year exponential decays and weighting them according to the proportion of animals of each sex that matured at each of these ages. The correction for an age-class was calculated as the geometric mean of $JCF_{s(x)}$ at age X and age X+1, which assumes that the metabolic rate evolved at a constant rate throughout the year. The correction was used to correct both basal (Eqn. 11) and maintenance (Eqn. 12) requirements.

One of the potential shortcomings in directly extrapolating the maintenance requirements of captive seals, $MR1$, to free-ranging seals is that normal activity patterns may be disrupted in captivity. For example, Innes et al. (1987) noted that some of the phocids included in their analysis were quiescent, and would thus be expected to have lower energy requirements than seals in the wild which spend a portion of their time foraging. A second estimate of gross maintenance requirements, $MR2_{s(x)}$, was therefore derived by weighting the metabolic rates of swimming, $SMR_{s(x)}$, and resting, $RMR_{s(x)}$, harbor seals according to a crude activity budget for free-ranging harbor seals:

$$MR2_{s(x)} = (P_s \cdot SMR_{s(x)}) + (P_r \cdot RMR_{s(x)}) \quad [13]$$

where P_s and P_r denote the proportion of time seals spend swimming and resting. P_s and P_r were set at 0.6 and 0.4 respectively based on the mean estimated percentage of time free-ranging radio-tagged harbor seals spent hauled out on land: 44% (Sullivan, 1979), 35–60% (Pitcher and McAllister, 1981) and 37% (Yochem et al., 1987). Age-specific swimming metabolic rates, $SMR_{s(x)}$, were inferred (see Results) from the swimming metabolic rates of captive harbor seals (Davis et al., 1985; Williams, 1987). Resting metabolic rates, $RMR_{s(x)}$, were assumed to be equivalent to $BMR_{s(x)}$ (appropriately elevated for juveniles). Since the extreme air and sea temperatures in the study area were likely within the thermoneutral zone, thermoregulatory costs were assumed to be negligible (see Results and General Discussion).

In addition to maintenance requirements, growing animals require energy for body growth. Daily energy requirements for growth for each sex- and age-class, $DGR_{s(x)}$, were calculated as

$$DGR_{s(x)} = CG \cdot GI_{s(x)} \quad [14]$$

where CG is the apparent gross cost of growth, 201 $W(kg \cdot d^{-1})^{-1}$, as given in Innes et al. (1987), and $GI_{s(x)}$ the daily growth increment of each sex- and age-class (i.e. $[M_{s(x+1)} - M_{s(x)}]/365$).

Finally, mature seals may invest additional energy in reproduction. For females, the total costs of reproduction were partitioned into: 1) foetal development; and 2) nursing. The net energy invested in foetal development was estimated from the mass and energetic density of term fetuses and the placenta. The net energy invested in lactation was estimated indirectly from the amount of energy transferred to nursing pups as reflected by changes in the total mass and body composition of pups between birth and weaning and their maintenance requirements, MR, while nursing. The energy content of the placenta and the energetic densities of neonate carcasses and of the mass gained during nursing were extrapolated from those reported for harp seals (Worthy and Lavigne, 1983). The MR of nursing pups was assumed to be the same as that of adults of equivalent mass ($2.0 \times BMR$) and growth of pups was assumed to be linear while nursing. Gross reproductive costs were estimated from net costs by assuming that the net efficiency of mothers was 70% (see above) and that for lactation, 95% of the energy in milk transferred to pups was metabolizable (Oftedal and Iverson, 1987). Since females deplete blubber reserves accumulated during the non-breeding season to meet these costs (Pitcher, 1986), age-specific daily reproductive requirements, $DRR_{(x)}$, were estimated by amortizing the annual cost over the entire year and applying it to female age-classes based on their fecundity rates, $FEC_{(x)}$. Since harbor seals are promiscuous and males are not known to fast or fiercely compete for breeding rights (Bigg, 1981), reproductive costs for males were assumed to be negligible and absorbed into their daily maintenance requirements.

Two estimates of daily food requirements, $FR_{(x)}$ in kg, were derived. The first estimate, $FR1_{s(x)}$, was obtained by summing the components of the energetic budget ($MR_{s(x)}$, $DGR_{s(x)}$ and, for females, $DRR_{(x)}$) to determine the total daily energy requirements, $DER_{s(x)}$. Estimates for each sex- and age-class were derived by taking the geometric mean of the parameters at age X and X+1, which assumes that the parameters changed at a constant rate throughout the year. $DER_{s(x)}$ was subsequently converted to units of biomass, $FR1_{s(x)}$ by dividing it by the mean weighted energetic density of

the diet. A second estimate, $FR2_{s(x)}$, was obtained directly from Boulva and McLaren's (1979) relationship between daily ingestion rates and body mass:

$$FR2_{s(x)} = 0.089 \cdot M_{s(x)}^{0.76} \quad \text{(from Fig. 2 in Boulva and McLaren, 1979) [15]}$$

based on the amount of undigested prey found in the stomachs of harbor seals collected on the east coast of Canada.

Diet composition

The diet of harbor seals in the study area was determined by scat analyses. During 1982–88, a total of 2,841 scats (216 collections) were collected from 58 sites (11 estuaries and 47 non-estuary sites) distributed throughout the Strait of Georgia (Fig. 1). Samples were collected in all months of the year (Fig. 2). Because most major haulout sites were sampled, the sampled sites accounted for about 45% of all seals observed during censuses of the study area both in May–June and in August, 1988. The collections thus provided a representative sample from which regional and seasonal variations in diet composition could be assessed.

Figure 2

Histograms showing (**A**) number of harbor seal scat samples collected; and (**B**) number of scat collections by month within and outside of estuaries.

Undigested prey remnants were recovered from the scat samples with an elutriator (Bigg and Olesiuk, 1990). Elutriation recovery rates ranged between 90–100% ($\bar{X}$=98.6%) for various fish structures and 70–100% ($\bar{X}$=85.0%) for cephalopod beaks. In contrast to previous scat studies which have relied almost exclusively on otoliths to identify prey, harbor seal prey were identified by using a wide array of different structures including otoliths, teeth, scutes and scales, as well as numerous cranial, appendicular, axial and caudal elements (see Appendix I in Olesiuk et al., 1990b).

The relative importance of prey in the diet was measured by using a new index, termed split-sample frequency of occurrence, designed specifically for scat analyses (Olesiuk et al., 1990b). The index was predicated on two assumptions: 1) prey identified in scat samples represented all those consumed in the previous meal (i.e., 24-hour period); and 2) all prey species constituting a meal had been consumed in equal volumes. Thus, the proportion of the diet comprised of the kth prey species in the jth strata (j=E for estuaries and j=O for outside estuaries) in the mth month (m=1 for January, etc.), P_{jkm}, was estimated from the i=1,..,n samples collected from that strata in that month by

$$P_{jkm} = \sum_{i=1}^{n} (O_{ijkm} / \sum_{k=1}^{N} O_{ijkm}) / n \quad k=1,..,N \quad \text{(N=\# different prey species) [16]}$$

where O_{ijkm} is a binary variate that indicates whether the kth prey species was absent or present (0=absent and 1=present) in the ith sample collected in the jth strata in the mth month, such that $\sum O_{ijkm}$ for k=1,..,N represents the total number of prey species present in the ith sample. Therefore, if only one prey species occurred in a sample, its occurrence was scored as 1, if two prey species occurred each occurrence was scored as 0.5, and so forth. The split-sample index is considered an improvement over conventional frequency of occurrence indices in that prey species that comprised an entire meal, which had presumably been consumed in large quantities, weighted the split-sample index more than prey species consumed in a diverse meal comprising many species, each of which had presumably been consumed in smaller quantities. Estimates of the diet composition on the tth date, P_{Ekt} and P_{Okt}, were derived by linearly interpolating between the monthly estimates, P_{Ekm} and P_{Okm}, plotted at the midpoint of each month.

Although it was not possible to assess the assumption that all prey in a meal had been consumed in equal volumes (see Results), the maximum potential biases introduced by deviations from the assumption could be determined. An upper limit of the importance of a particular prey species in the overall diet was obtained by assuming that whenever the species occurred in a meal, it comprised the entire meal and that all other species in the same meal had been consumed in negligible quantities. Conversely, a lower limit was obtained by assuming that whenever a particular species was consumed in the same meal along with other species, it had been consumed in negligible quantities. Mathematically, the upper and lower limits for the lth of k=1,...,N species were calculated from Equation 16 by

1) Setting O_{ijkm}=1 for k=l and O_{ijkm}=0 for $k \neq l$;
2) Setting O_{ijkm}=0 for k=l and O_{ijkm}=1 for $k \neq l$ when N>1,

respectively.

Two corrections were applied to the split-sample index to account for suspected biases. First, very small scat samples, which undoubtedly represented only a small fraction of whole scats and probably contained only a portion of all the prey species actually consumed in meals, were weighted less than large scat samples. Second, the relative proportions of hake and herring, the two predominant prey species, in samples that contained both species were volumetrically weighted based on the mean relative number of elements of each species in the sample compared with the relative number in samples that were composed exclusively of each of these two species. Both corrections, each of which had a relatively minor influence on the results, are described in detail in Olesiuk et al. (1990b).

Results

Abundance and distribution

The two complete censuses of the study area in 1988, when adjusted to post-pupping levels and corrected for missed seals (Eqn. 3), yielded population estimates of 16,531 and 15,091, respectively. Their mean, 15,810, was adopted in subsequent analyses. The mean was considered most appropriate because the proportion of the population counted during any single census may have been lower or greater than the mean estimate of 0.884. The validity of the 1988 census estimate was substantiated by a projected population estimate of 15,050 based on population trends during 1973–88, over which period the population had been steadily increasing (log-linear r^2=0.994) at a rate of 12.5% per annum (Olesiuk et al., 1990a).

Seasonal fluctuations in the size of population as a result of mortality and recruitment are shown in Figure 3A. The total size of the population ranged from a low of 12,990 just prior to the pupping season (16 June) to a peak of 15,810 at the end of the pupping season (6 September). The mean size of the population was 14,270. Because the population was below carrying capacity and increasing at its intrinsic rate, it was 12.5% larger at the end than at the beginning of the year.

Seasonal changes in the distribution of harbor seals between estuaries and non-estuaries are shown in Figure 3B. The overall abundance within estuaries was lowest (4% of the total population) in December and remained low throughout the winter and into early spring. Numbers increased sharply during June–August, mainly due to large influxes into the two largest estuaries—Boundary Bay and lower Fraser River (Fig. 1). These influxes coincided with the pupping season (Bigg, 1969; Olesiuk et al., 1990a) which might indicate these two large estuaries were preferred whelping areas, as has been reported for other major es-

Figure 3

Seasonal fluctuations in (**A**) the total size of the Strait of Georgia harbor seal population, N_t, due to recruitment and mortality; and (**B**) the total number of seals inhabiting estuaries, N_{Et}. Note that the two parameters are plotted on different scales.

tuaries along the coast of Washington and Oregon (Jefferies[5]). Alternatively, these influxes also coincided with the earliest low tides of the year in which the sandbars utilized as haulouts were exposed during daylight hours and may therefore merely indicate that seals preferred to occupy areas where they could haulout during daylight.

Although numbers in Boundary Bay declined after August (i.e., the end of the pupping season), the overall proportion of the population in estuaries continued to increase and peaked at 18% in September. This was due largely to a migration of seals from Boundary Bay to the Fraser River and an influx of seals into many of the smaller estuaries, where peak abundance generally occurred in September–November coinciding with the return of spawning salmon to their natal rivers (Olesiuk et al., 1990b). Weighted seasonally, 10.3% of the total population inhabited estuaries.

Population parameters

As expected, the relative number of animals in age-classes decreased with age (Fig. 4). However, piecewise log-linear regressions indicated that the rate of decline for both sexes changed abruptly at 4 years of age, which roughly coincided with the onset of sexual maturity (see Tables 1 and 2). The regressions for females and males aged 1–4 years were not significantly different (t=0.18; P>0.50), so juveniles of both sexes were pooled. For females, the rate of decline decreased beyond age 4 years, whereas for males the rate increased beyond age 4 years:

$$N_{s(x+t)}=N_{s(x)}e^{-0.2175t} \quad \text{for both sexes aged 1–4 year [17]}$$
$$N_{f(x+t)}=N_{f(x)}e^{-0.1653t} \quad \text{for females aged >4 years [18]}$$
$$N_{m(x+t)}=N_{m(x)}e^{-0.2878t} \quad \text{for males aged >4 years [19]}$$

The $N_{s(x)}$ series were truncated at 29 years for females and 20 years for males. The truncation points, MA_f and MA_m, represent the oldest specimens collected by Bigg (1969) and also the ages by which the size of age-classes diminished to less than 0.5% the number of new recruits (see Tables 1 and 2). It should be noted that the rates of decline in the size of age-classes do not entirely reflect mortality because the population was non-stationary, such that the number of seals being recruited (i.e., the initial size of cohorts) had increased over time. When corrected for an intrinsic rate of increase of 12.5% per annum (Olesiuk et al., 1990a), the exponential decays represent finite annual mortality rates of 9.5% for juveniles aged 1–4 years, 4.6% for adult females aged >4 years and 15.6% for adult males aged >4 years (Olesiuk[3]). The finite *per capita* birth rate, β, was calculated to be 29.8%, which implied that mortality during the first year was 27.0%. The finite *per capita* mortality rate, ∂, was subsequently estimated to be 13.3%.

The estimated number of seals in each sex- and age-class indicates that the population was markedly skewed toward younger age-classes (see Tables 1 and 2). The mean age was only 4.0 years (4.7 years for females and 3.2 years for males). A total of 74% of all individuals were aged ≤5 years and 91% were aged ≤10 years. As noted previously, this skewed age-structure was not due entirely to high mortality (mean life expectancy was 8.2 years—10.4 years for females and 6.0 years for males; Olesiuk[4]), but also because the population had been exponentially increasing since 1970 (Olesiuk et al., 1990a). Given a growth rate of 12.5%, the total population numbered only 8,770 in 1983 and 4,870 in 1978, such that the initial size of the 1983 cohort, represented by 5-year-olds in the population in 1988, was only 55% the intial size of the 1988 cohort, and the initial size of the 1978 cohort, represented by 10-year-olds in the population in 1988, only 31% the initial size of the 1988 cohort. In other words, the population in 1988 was skewed toward younger animals because most of its constituents had been recruited in recent years.

Bigg (1969) reported that mean body mass of pups increased from 10.2 kg at birth to 24.0 kg by the end of the 5–6 week nursing period, but there appeared to be little further increase in body mass during the

[5]Jefferies, S. J. 1986. Seasonal movements and population trends of harbor seals (*Phoca vitulina richardsi*) in the Columbia River and adjacent waters of Washington and Oregon. Final Rep. Mar. Mammal Comm., Contr. No. MM2079357-5, 41 p.

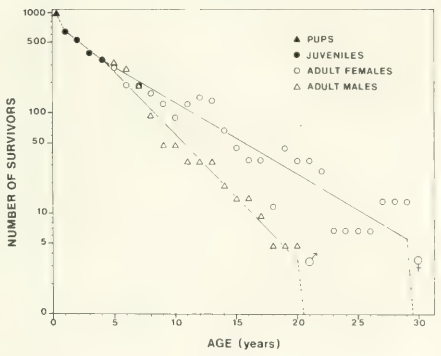

Figure 4

Exponential rates of decline in the size of age-classes of harbor seals as a function of age (Olesiuk[4]). The trend lines represent piecewise log-linear functional regressions fitted by least squares criteria and scaled to an initial cohort size of 1000.

Table 1

Energetic life table for males. Parameters are: $N_{m/s/}$ number in age-class; $M_{m/s/}$ mean body mass (kg); $MAT_{m/s}$ proportion of animals mature; $JCF_{m/s}$ multiplier to correct for elevated juvenile metabolic rates; $BMR_{m/s/}$ basal metabolic rate; $MR1_{m/s/}$, $MR2_{m/s/}$, and $\overline{MR}_{m/s/}$ gross maintenance requirements based on ingestion rates in captivity, daily activity budgets, and their average respectively; $DGR_{m/s/}$ mean daily growth requirements; $DER_{m/s/}$ mean daily total energy requirements; and $FR1_{m/s/}$, $FR2_{m/s/}$ and $\overline{FR}_{m/s/}$ daily food requirements (kg) based on energetic life tables, volumes of stomach contents, and their average respectively. Parameters are given for the population of 15,810 at the end of the pupping season. All energetic parameters are in watts.

Age	$N_{m/s/}$	$M_{m/s/}$	$MAT_{m/s/}$	$JCF_{m/s}$	$BMR_{m/s/}$	$MR1_{m/s/}$	$MR2_{m/s/}$	$\overline{MR}_{m/s/}$	$DGR_{m/s/}$	$DER_{m/s/}$	$FR1_{m/s/}$	$FR2_{m/s/}$	$\overline{FR}_{m/s/}$
0	1814	24.0	0.00	1.80	67.1	130.3	170.5	150.4	2.9	153.4	1.99	1.07	1.53
1	1178	29.3	0.00	1.60	71.4	137.3	181.4	159.4	5.3	164.6	2.14	1.29	1.71
2	948	38.9	0.00	1.42	76.9	146.3	195.3	170.8	5.5	176.3	2.29	1.57	1.93
3	762	48.9	0.06	1.26	79.5	150.2	202.0	176.1	4.7	180.8	2.35	1.82	2.08
4	613	57.5	0.29	1.13	80.4	151.1	204.3	177.7	3.9	181.6	2.36	2.02	2.19
5	460	64.5	0.53	1.05	81.5	152.5	207.0	179.7	3.1	182.9	2.38	2.18	2.28
6	345	70.2	1.00	1.00	84.1	156.8	213.5	185.2	2.5	187.6	2.44	2.31	2.37
7	259	74.6	1.00	1.00	87.5	162.9	222.3	192.6	1.9	194.5	2.53	2.40	2.46
8	194	78.1	1.00	1.00	90.1	167.5	228.9	198.2	1.5	199.7	2.59	2.47	2.53
9	145	80.8	1.00	1.00	92.1	171.0	234.0	202.5	1.1	203.6	2.65	2.53	2.59
10	109	82.8	1.00	1.00	93.7	173.7	237.9	205.8	0.9	206.6	2.68	2.57	2.63
11	82	84.4	1.00	1.00	94.8	175.7	240.8	208.3	0.6	208.9	2.71	2.60	2.66
12	61	85.5	1.00	1.00	95.7	177.2	243.0	210.1	0.5	210.6	2.74	2.63	2.68
13	46	86.4	1.00	1.00	96.3	178.4	244.7	211.5	0.4	211.9	2.75	2.65	2.70
14	34	87.1	1.00	1.00	96.8	179.2	245.9	212.6	0.3	212.9	2.77	2.66	2.71
15	26	87.6	1.00	1.00	97.2	179.9	246.9	213.4	0.2	213.6	2.77	2.67	2.72
16	19	88.0	1.00	1.00	97.5	180.4	247.6	214.0	0.2	214.1	2.78	2.68	2.73
17	15	88.3	1.00	1.00	97.7	180.7	248.1	214.4	0.1	214.5	2.79	2.68	2.74
18	11	88.5	1.00	1.00	97.8	181.0	248.5	214.7	0.1	214.8	2.79	2.69	2.74
19	8	88.7	1.00	1.00	97.9	181.2	248.8	215.0	0.1	215.1	2.79	2.69	2.74
20	6	88.8	1.00	1.00	98.0	181.3	248.9	215.1	0.1	215.2	2.80	2.69	2.74

Table 2

Energetic life table for females. Parameters are the same as described in Table 1 with the following additions: $FEC_{f/}$ annual fecundity rate; and $DRR_{f/}$ mean daily gross reproductive requirements. Parameters are given for the population of 15,810 at the end of the pupping season. All energetic parameters are in watts.

Age	$N_{f/}$	$M_{f/}$	$MAT_{f/}$	$JCF_{f/}$	$BMR_{f/}$	$MR1_{f/}$	$MR2_{f/}$	$\overline{MR}_{f/}$	$DGR_{f/}$	$FEC_{f/}$	$DRR_{f/}$	$DER_{f/}$	$FR1_{f/}$	$FR2_{f/}$	$\overline{FR}_{f/}$
0	1814	24.0	0.00	1.80	65.8	127.8	167.2	147.5	2.9	0.00	0.0	150.4	1.95	1.07	1.51
1	1178	29.3	0.00	1.54	65.4	125.9	166.0	146.0	3.7	0.00	0.0	149.6	1.94	1.25	1.60
2	948	36.0	0.00	1.31	64.9	124.1	164.9	144.5	4.3	0.00	0.0	148.8	1.93	1.46	1.70
3	762	43.9	0.36	1.12	64.8	123.0	164.7	143.8	3.4	0.29	9.6	156.9	2.04	1.66	1.85
4	613	50.0	0.83	1.02	66.5	125.6	168.9	147.2	2.5	0.66	22.1	171.9	2.23	1.80	2.02
5	520	54.5	1.00	1.00	69.5	131.0	176.5	153.8	1.8	0.79	26.5	182.1	2.37	1.90	2.13
6	441	57.9	1.00	1.00	72.2	135.7	183.3	159.5	1.3	0.91	30.7	191.6	2.49	1.97	2.23
7	374	60.2	1.00	1.00	74.0	139.0	188.1	163.5	0.9	0.91	30.7	195.2	2.54	2.03	2.28
8	317	62.0	1.00	1.00	75.4	141.4	191.4	166.4	0.7	0.91	30.7	197.8	2.57	2.06	2.32
9	268	63.2	1.00	1.00	76.3	143.0	193.8	168.4	0.5	0.91	30.7	199.6	2.59	2.09	2.34
10	227	64.0	1.00	1.00	76.9	144.2	195.4	169.8	0.3	0.91	30.7	200.9	2.61	2.11	2.36
11	193	64.6	1.00	1.00	77.4	145.0	196.6	170.8	0.2	0.91	30.7	201.7	2.62	2.12	2.37
12	163	65.0	1.00	1.00	77.7	145.5	197.4	171.5	0.2	0.91	30.7	202.4	2.63	2.13	2.38
13	139	65.3	1.00	1.00	77.9	145.9	197.9	171.9	0.1	0.91	30.7	202.8	2.63	2.13	2.38
14	117	65.5	1.00	1.00	78.1	146.2	198.3	172.3	0.1	0.91	30.7	203.1	2.64	2.14	2.39
15	100	65.6	1.00	1.00	78.2	146.4	198.6	172.5	0.1	0.91	30.7	203.3	2.64	2.14	2.39
16	84	65.7	1.00	1.00	78.3	146.5	198.8	172.6	0.0	0.91	30.7	203.4	2.64	2.14	2.39
17	72	65.8	1.00	1.00	78.3	146.6	198.9	172.8	0.0	0.91	30.7	203.5	2.64	2.15	2.39
18	61	65.9	1.00	1.00	78.3	146.7	199.0	172.8	0.0	0.91	30.7	203.6	2.65	2.15	2.40
19	51	65.9	1.00	1.00	78.4	146.7	199.1	172.9	0.0	0.91	30.7	203.7	2.65	2.15	2.40
20	44	65.9	1.00	1.00	78.4	146.8	199.1	172.9	0.0	0.91	30.7	203.7	2.65	2.15	2.40
21	37	65.9	1.00	1.00	78.4	146.8	199.1	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
22	31	65.9	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
23	27	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
24	22	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
25	19	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.7	2.65	2.15	2.40
26	16	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40
27	14	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40
28	12	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40
29	10	66.0	1.00	1.00	78.4	146.8	199.2	173.0	0.0	0.91	30.7	203.8	2.65	2.15	2.40

remainder of the first year of life. The average body mass of 12 yearlings (7 females and 5 males) aged 1.0 years (±2 months) was 29.3 kg (28.4 kg for females; 30.7 kg for males). Growth in subsequent years was asymptotic for both sexes and could be described by von Bertalanffy curves (Fig. 5). The equations indicated that females attained an asymptotic mass of 66.0 kg, 90% of which was attained by 7 years, and males an asymptotic mass of 89.2 kg, 90% of which was attained by 9 years. In accord with these predictions, the mean body mass of the 10 female specimens aged ≥7 years was 60.0 kg and the mean of the 8 male specimens aged ≥9 years was 86.6 kg (Fig. 5). The mean body mass of all ages, calculated at the end of the pupping season and weighted according to the stable age-structure, was 44.2 kg for females, 45.3 kg for males, and 44.7 kg overall.

Energetics

Energetic life tables are shown in Tables 1 and 2. The main advantage of the energetics approach over stomach volume analyses was that total energy requirements could be partitioned into energy required for basal metabolism, activity, growth and reproduction. This enabled an assessment of the relative magnitude and uncertainty associated with each component of the energy budget.

The estimated gross maintenance requirements of adult harbor seals, based on the rate of energy ingestion by captive phocids, $MR1_{s(x)}$, ranged from 1.85–1.94× ($\bar{X}$=1.90×) the predicted adult *BMR* (Eq. 11).

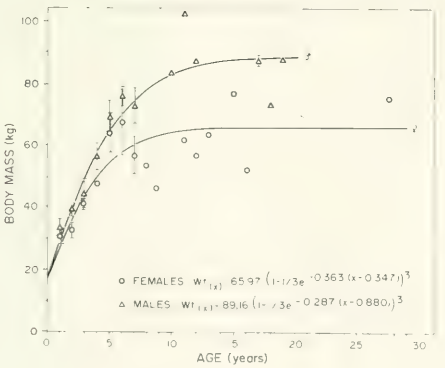

Figure 5

Mean body mass (±SE) as a function of age. Data are from Bigg (1969) supplemented with data from Bishop (1967). Growth curves represent specialized von Bertalanffy equations fitted to the data by least squares criteria.

Multipliers to account for the elevated metabolic rates of juveniles, $JCF_{s(x)}$ ranged from 1.8 at weaning to 1.0 at the onset of maturity. The corrected juvenile maintenance requirements, $MR1_{s(x)}$, thus declined from 3.5× the predicted adult *BMR* at weaning, to 3.1× the predicted adult *BMR* at age 1.0 years, to 2.6× the predicted adult *BMR* at age 2.0 years, and ultimately to 1.9× the predicted adult *BMR* at the onset of maturity. These predictions appear to be consistent with the metabolic rates of juveniles reported in the literature. Keiver et al. (1984) reported that the gross maintenance requirements of harp seals aged 5–24 months were 2.1–3.0× predicted adult *BMR* levels and data in Innes (1984) indicate that the gross maintenance requirements (assuming 70% net efficiency) of grey and harp seals aged 1–28 months were 2.9× predicted adult *BMR* levels. The unweighted mean correction for juveniles of all ages was 1.34, which was similar to the 1.4 derived by Innes et al. (1987) for juveniles of various ages pooled. Similarly, the average $MR1_{s(x)}$ for harbor seals aged 0–3 years was 2.9× the predicted adult *BMR*, which was similar to the 2.8× adult *BMR* estimated for captive harbor seals aged 0–3 years by Markussen et al. (1990) who, interestingly, found no evidence of age-specific changes in maintenance requirements between 0 and 3 years of age.

A second estimate of maintenance requirements, *MR2*, was obtained by weighting swimming and resting metabolic rates, *SMR* and *RMR*, according to an activity budget for free-ranging harbor seals. Davis et al. (1985) reported that the *SMR* of a 63-kg adult harbor seal swimming at 1.4 m·sec^{-1}, its preferred swimming speed, was 2.3× its expected *BMR* (i.e., 2.2× its resting metabolic rate which was reported to be 1.1× *BMR*). Similarly, the net *SMR* of an 85-kg adult harbor seal swimming at the same speed was 210 watts (Williams, 1987), or 2.4× its predicted *BMR*. In contrast, a 33-kg yearling swimming at 1.4 m·sec^{-1} exhibited a relatively higher net swimming metabolic rate of 170 watts (Davis et al., 1985). Although this was 3.6× the predicted *BMR* for an adult of equivalent mass, it was only 2.3× the corrected *BMR* for a yearling (i.e., the juvenile *SMR* appeared to be elevated to the same extent as its total *MR1*). Age-specific $SMR_{(x)}$'s were therefore assumed to be 2.3× $BMR_{s(x)}$ (appropriately elevated for juveniles) for all ages and both sexes. Assuming that seals spent 40% of their time resting on land and 60% swimming and that the $RMR_{(x)}$'s were equivalent to $BMR_{s(x)}$ (again appropriately elevated for juveniles), the net $MR2_{s(x)}$ was estimated to be 1.8× the corrected $BMR_{s(x)}$, and the gross $MR2_{s(x)}$ to be 2.5× the corrected $BMR_{s(x)}$.

The second estimate of gross maintenance requirements, *MR2*, was approximately 34% (range 31–37%) greater than the first estimate, *MR1*, for all age-classes.

As noted earlier, *MR1* probably tended to be an underestimate as it was derived from captive seals that were sometimes quiescent. On the other hand, *MR2* may be an overestimate as it is unlikely that seals swim continuously while in the water, and also because the *RMR* of sleeping seals may actually fall below *BMR* (Ashwell-Erickson and Elsner, 1981; Worthy, 1987a). The mean of $MR1_{s(x)}$ and $MR2_{s(x)}$, denoted as $\overline{MR}_{s(x)}$, was therefore adopted for subsequent calculations.

Ambient sea and air temperatures in the study area were probably within the thermoneutral zone of free-ranging harbor seals. Oritsland and Ronald (1975) detected no change in the metabolic rate of an adult harp seal swimming in water temperatures ranging from 8.5–26°C and Gallivan (1977) no change in the metabolic rates of 3 adult harp seals in water temperatures ranging from 1.8 to 28.2°C. Hart and Irving (1959) reported that the lower critical temperature of harbor seals in air was 2°C and Matsuura and Whittow (1973) found that the metabolic rate of a resting harbor seal was constant in air temperatures up to 35°C. Mean monthly sea surface temperatures in the study area typically range between 6.2 and 17.0°C[9] and minimum and maximum monthly air temperatures between –0.4 (January minimum) and 23.5°C (July maximum) (Canadian Hydrographic Service, 1990). Thermoregulatory costs were therefore assumed to be negligible (see also General Discussion).

The costs associated with growth were calculated based on actual growth rates rather than applying Innes' et al. (1987) empirical equations for growing phocids because there may be substantial differences between growth rates of captive and free-ranging seals. For instance, growth rates reported for recently weaned grey and harp seals in captivity (Worthy, 1987a) were about an order of magnitude greater than those estimated for harbor seals in the wild. The apparent gross cost of growth, $201\ W(\mathrm{kg \cdot d^{-1}})^{-1}$ (Innes et al., 1987), represents, assuming net efficiency was 70%, a net cost of $141\ W(\mathrm{kg \cdot d^{-1}})^{-1}$ or 12.2 $\mathrm{MJ \cdot kg^{-1}}$. Given the wet-weight energetic density of tissues (37.8 $\mathrm{MJ \cdot kg^{-1}}$ for blubber and 6.5 $\mathrm{MJ \cdot kg^{-1}}$ for proteinaceous tissue; Olesiuk and Bigg, unpubl. data), this implies that post-weaning body growth was composed of about 20% fat and 80% protein. Using these values to extrapolate the estimated body composition at weaning (see below), the adult body would be composed of approximately 30% blubber, which is consistent with the 27–30% reported for free-ranging harbor seals (Pitcher, 1986). Daily growth requirements, $DGR_{s(x)}$, were low for all age-classes, ranging from about 2.5–5.5 watts for juveniles to negligible values for adults.

[9]H. Freeland, Institute of Ocean Sciences, Pat Bay, B.C., pers. commun. 1989.

In calculating the energy invested in foetal development, the energetic density of the fetus was assumed to be the same as the 7.2 $\mathrm{MJ \cdot kg^{-1}}$ reported for harp seal neonates (Worthy and Lavigne, 1983). This implies that neonates are essentially devoid of fat, which is probably true as neonate and near-term harbor seals have very thin blubber layers (Pitcher, 1986). In addition, neonates can tolerate little mass loss before dying (Boulva and McLaren, 1979). Applying this value to the mean mass at birth of 10.2 kg (Bigg, 1969), the total energy content of the term foetus is estimated to be about 73.4 MJ. If it is assumed that, as in harp seals (Worthy and Lavigne, 1983), the placenta contains an additional 5.9 MJ, the net foetal investment is estimated at 79.3 MJ, and the gross investment at 113 MJ. Additional energy would be required for the metabolism of the fetus. However, the foetal mass would represent only a negligible portion of a female's total mass through most of the pregnancy. Moreover, since the foetal masses were not subtracted from the total masses of pregnant females incorporated into the growth curves, it was assumed that the costs were absorbed into the maintenance requirements of adult females.

In calculating the costs invested in lactation, the energetic density of the mass gained by pups was assumed to be the same as the 33.1 $\mathrm{MJ \cdot kg^{-1}}$ reported for harp seal pups (Worthy and Lavigne, 1983), which implies that the mass gained was approximately 85% fat and 15% protein. In view of their rapid rate of growth, this value is probably also applicable to nursing harbor seal pups. When applied to the 13.8 kg increase between the mean birth and weaning mass (10.2 and 24.0 respectively; Bigg, 1969), the energy assimilated by nursing pups is estimated to be 456.8 $\mathrm{MJ \cdot pup^{-1}}$. In addition, each nursing pup would require about 172.4 MJ for maintenance during the 5-1/2 week nursing period (Bigg, 1969). Thus, the total net nursing investment was estimated to be 629.2 MJ, which represents a gross investment of 946 MJ. The total annual cost of foetal development and lactation was thus estimated to be about 1060 MJ for each reproductive female.

Estimates of the total daily energy requirements, $DER_{s(x)}$, were surprisingly constant with age, ranging from 150 W for yearlings of both sexes to 215 W for full-grown males (Tables 1 and 2). The range in $DER_{s(x)}$ was much narrower (1.4×) than the range in body mass (3.7×) because the major energy expenditures scaled to $M^{0.75}$, and also because juvenile metabolic rates were elevated relative to adults of equivalent mass. The mean *per capita DER* was estimated to be 172 W.

Most of the daily energy requirement, *DER*, was expended for maintenance and comparatively little for

production. Daily growth requirements accounted for, on average, only 1.2% of the total gross *DER* (1.7% of NE), and only 2.1% (3.0% of NE) of the gross *DER* for seals aged 1–2 years which exhibited the highest growth costs. However, the estimates reflect only the direct costs associated with growth. A portion of the elevated metabolic rates of juveniles, which account for 8.4% of the overall population energy budget (12.0% of NE) but were incorporated into maintenance costs, may be indirectly associated with growth. Although the *DER* of lactating females were 2.8× those of non-lactating females of equivalent mass, and lactation accounted for 89% of the total costs of reproduction, lactation accounted for only 14.6% of the overall energy requirements of reproductive females when amortized over the entire year. Overall, net reproductive costs accounted for only 3.2% of the total population energy budget (4.5% of NE). Thus, growth and reproduction combined accounted for only 4.4% of the total population energy budget (6.2% of NE).

With respect to maintenance, basal metabolism accounted for 33.9% of the total population energy budget (48.4% of NE) when the corrections for elevated juvenile levels are excluded, or 42.3% (60.4% of NE) when the corrections are included. If it is assumed that 13% of gross maintenance requirements is lost in faeces and urine and 17% expended in the heat increment associated with feeding, and thermoregulatory costs were negligible, the remaining 23.4% of the total population energy budget (33.4% of NE) was expended on activity. However, there is considerable uncertainty in this estimate. Had total maintenance costs been directly extrapolated from captive animals using *MR1*, only 16.1% of the total budget (23.0% of NE) would have been available for activity. On the other hand, had total maintenance been estimated from the activity budget using *MR2*, 29.0% of the total budget (41.4% of NE) would have been available for activity. Averaging *MR1* and *MR2* thus introduced a potential error of about ±13% into the overall population energy budget.

Based on the energetic densities of 10 of the 15 most important prey species, which accounted for 86.1% of the overall diet, the mean weighted energetic density of the diet was estimated to be 6.65 MJ kg^{-1} (see Table 3). The total daily energy requirements, $DER_{s(x)}$, therefore translated into daily food requirements, $FR1_{s(x)}$, ranging from 2.0 kg for yearlings of both sexes to 2.8 kg for full-grown males (Tables 1 and 2), which represented 8.2% and 3.1% of their mean body masses respectively. The mean daily *per capita* food requirement, weighted according to the sex- and age-structure of the population, was estimated to be 2.2 kg, or 5.0% of mean body mass.

Estimates of daily food requirements based on the volumes of stomach contents, $FR2_{s(x)}$, were consistently lower than the estimates based on energetic life tables, $FR1_{s(x)}$ (Fig. 6). The mean *per capita* food requirement estimate based on stomach volumes, *FR2*, was 1.6 kg, or 73% of the mean estimated of 2.2 kg based on energetic life tables, *FR1*. It is unlikely that much of the discrepancy between the two estimates can be attributed to differences in the energetic density of diets on the east and west coasts. A crude estimate of the mean energetic density of the east coast diet, obtained by applying energetic densities of similar species on the west coast to 10 of the 15 most important prey on the east coast, which combined accounted for 81.2% of the east coast diet, was 6.31 MJ kg^{-1}, or 95% of the diet in the study area.

The magnitude of the discrepancy between $FR1_{s(x)}$ and $FR2_{s(x)}$ declined with age (Fig. 6). There was fairly good agreement between the two methods for adults: 2.1 kg from stomachs versus 2.5 kg from energetic life tables. The former was almost within the ±13% potential error introduced in the latter owing to uncertainty in the costs associated with activity (see above). In contrast, juvenile estimates based on stomach volumes were substantially lower than corresponding estimates based on the energetic life tables (Fig. 6). The average *per capita* requirement for immature seals based on stomachs, 1.3 kg, was only 65% of the estimate based on energetic life tables, 2.1 kg. The estimate based on stomach volumes for yearlings, the age-class exhibiting the greatest discrepancy, was only 52% of the estimate based on energetic life tables. The reason for the larger discrepancy for immature age-classes was that the volumes of stomachs, when all ages were pooled, was scaled to $M^{0.76}$ (Eqn. 15), which was close to the $M^{0.75}$ expected for adults (Eqn. 11). In other words, there was no evidence that juveniles consumed greater quantities of prey than adults of equivalent mass, whereas significant corrections were applied in the energetic life tables to account for the elevated metabolic rates of juveniles.

One factor that might have contributed to this discrepancy may have been post-weaning changes in body composition. At weaning, about 50% of body mass of pups is composed of blubber which, as the animal ages, is used and displaced by proteinaceous tissue. Thus, although pups exhibited some post-weaning growth in body mass during the first year, they may actually have experienced negative growth in energetic terms. However, even if it is assumed that all of the post-weaning blubber reserves (37.8 MJ·kg^{-1}) were replaced with proteinaceous tissue (6.5 MJ·kg^{-1}) during the first year, the daily energy requirement of yearlings would decrease by only 0.15 kg day^{-1}, or 15% of the observed discrepancy.

The discrepancy between $FR1_{s(x)}$ and $FR2_{s(x)}$ for juveniles suggests that the metabolic rates of free-living

Table 3

Contribution to the overall diet (upper and lower limits), estimated annual consumption in metric tons (range), and energetic density ($MJ \cdot kg^{-1}$) of harbor seal prey in the Strait of Georgia. The range in annual consumption was calculated by assuming that daily food requirements were within ±35% of the point estimate and that realistic upper and lower limits of the importance of prey in the diet were half the width of the extreme limits (see Discussion). Energetic densities are from Perez and Bigg (1986) converted to joules assuming 1 calorie = 4.184 joules.

Prey species	Percentage of overall diet	Annual prey consumption (t)	Energetic density
Pacific hake (*Merluccius productus*)	42.6 (26.3–57.2)	4,214 (2,215–6,664)	4.90
Pacific herring (*Clupea pallasi*)	32.4 (19.8–54.7)	3,206 (1,679–5,818)	9.08
Pacific salmon (*Oncorhynchus* spp.)	4.0 (1.3– 8.6)	398 (171– 846)	8.41
Plainfin midshipman (*Porichthys notatus*)	3.4 (0.8– 7.8)	335 (135– 745)	—
Lingcod (*Ophiodon elongatus*)	3.0 (1.3– 5.4)	294 (137– 556)	—
Surfperches (Family Embiotocidae)	2.3 (0.5– 5.4)	230 (91– 520)	—
Cephalopods (Class Cephalopoda)	2.1 (0.0– 5.9)	208 (68– 535)	[1]5.06
Flatfishes (Order Pleuronectiformes)	1.2 (0.5– 2.9)	123 (57– 284)	5.02
Sculpins (Family Cottidae)	1.2 (0.1– 3.1)	114 (40– 276)	—
Rockfishes (Family Scorpaenidae)	1.1 (0.4– 2.4)	112 (50– 241)	4.90
Pacific tomcod (*Microgadus proximus*)	1.0 (0.6– 1.4)	101 (53– 164)	—
Walleye pollock (*Theragra chalcogramma*)	1.0 (0.6– 1.3)	97 (50– 151)	5.90
Pacific sand lance (*Ammodytes hexapterus*)	0.8 (0.4– 2.1)	79 (39– 193)	5.10
Pacific cod (*Gadus macrocephalus*)	0.5 (0.3– 0.7)	54 (28– 87)	4.18
Smelts; mainly eulachon (Family Osmeridae)	0.4 (0.3– 1.8)	40 (23– 149)	[2]5.90
Unidentified/other fishes	2.7 (1.0– 3.0)	267 (119– 380)	—
Other invertebrates	0.2 (0.0– 0.6)	20 (7– 54)	—
Total consumption / Weighted mean energetic density		9,892 (6,432–13,359)	6.65

[1]Mean of values for market and gonatid squid.
[2]Value for eulachon, the dominant smelt in the diet.

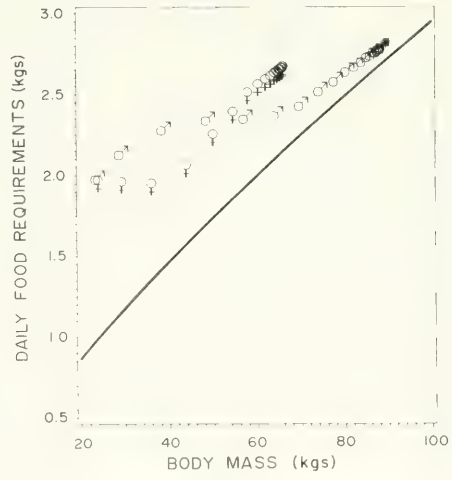

Figure 6

Comparison of estimates of daily food requirements for each sex- and age-class based on energetic life tables, *FR1* (sex symbols), and those based on the volumes of undigested prey in harbor seal stomachs collected on the east coast of Canada, *FR2* (trend line; from Boulva and McLaren 1979).

juveniles may not be as elevated or may converge on adult rates more rapidly than those of captive juveniles. For example, the magnitude by which juvenile metabolic rates are elevated may be a function of their growth rates, which were generally much higher in captivity than in free-ranging harbor seals. Alternatively, the elevated metabolic rates of juveniles may have been obscured in Boulva and McLaren's (1979) analysis by the indiscriminate pooling of juveniles and adults, or the average meal sizes of juveniles underestimated due to seasonal biases. For instance, most of Boulva and McLaredn's (1979) specimens were collected in summer and fall, which coincides with a post-weaning reduction in food intake in several other species of phocids (Worthy, 1987b).

In the absence of any compelling basis for favouring either $FR1_{s(x)}$ or $FR2_{s(x)}$, their mean, denoted as $\overline{FR}_{s(x)}$, was adopted in subsequent analyses. Since juvenile $FR1_{s(x)}$ and $FR2_{s(x)}$ differed by about ±20% of their mean, and juveniles accounted for 62% of the total population energy budget, this introduced a potential error of ±12% into the overall population energy budget. Estimated daily food requirements, $\overline{FR}_{s(x)}$, ranged from 1.5 kg for yearlings to 2.7 kg for full grown males, which represented 6.3% and 3.1% of their total body masses respectively. The mean *per capita* daily food requirement, $\overline{FR}$, was estimated to be 1.9 kg, or 4.3% of mean body mass.

Diet composition

Of the 2,841 scat samples collected in the Strait of Georgia, 2,765 (97.3%) contained identifiable prey. Samples typically contained one to three ($\bar{X}$=1.91) different prey species, but occasionally contained as many as seven. Marine and anadromous fishes, which accounted for 96.0% of all prey identified, were by far the most prevalent prey category. The diet included at least 48 species from 20 different families (Olesiuk et al., 1990b). The diet was dominated by gadoids and clupeids which were present in 62.0 and 59.2%, respectively of all samples containing identifiable prey. Other important families that occurred in at least 1% of samples were, in decreasing order of importance, salmonids, batrachoids, embiotocids, cottids, pleuronectids, hexagrammids, scorpaenids, ammodytids and osmerids.

The second most prevalent prey category was cephalopods, which occurred in 168 (6.1%) of all samples containing identifiable prey and represented 3.5% of all prey items identified. A superficial examination of their beaks indicated that the vast majority were squid (mainly *Loligo opalacens* with lesser amounts of *Gonatus* spp.), but at least one octopus was also consumed. The remaining prey categories, namely crustaceans, other molluscs, echinoderms, and birds, occurred in <1% of all samples containing identifiable prey and accounted for <0.5% of the total number of prey items identified.

In assessing the relative importance of each prey (Eqn. 16), it was assumed that scats represented all prey consumed within a 24-hour period. Since pinniped gastrointestinal passage rates typically range from 5 to 30 hours (Pastukhov, 1975; Helm and Morejohn, 1979; Prime, 1979; Bigg and Fawcett, 1985; Prime and Hammond, 1987; Harvey, 1989), it is likely that most of the prey present in a scat sample had been consumed within the same 24-hour period. Although cephalopod beaks may be retained in stomachs over longer periods (Bigg and Fawcett, 1985), cephalopods constituted only a small part of the diet and beaks were usually accompanied by cephalopod eye lenses, which probably pass rapidly.

It is believed that essentially all species consumed in a meal were represented in scat samples, mainly because such a wide array of structures had been used to identify prey. Captive studies of otolith recovery rates have indicated that the fragile otoliths of small fishes, such as herring, may be completely digested and hence under-represented in scats (Hawes, 1983; Jobling and Breiby, 1986; Jobling, 1987; da Silva and Neilson, 1985; Dellinger and Trillmich, 1988; Harvey, 1989). Furthermore, based on a comparison between harbor seal stomach and intestinal contents, Pitcher (1980) concluded that the otoliths of larger prey such as salmon would also tend to be under-represented in scats because their heads (i.e., otoliths) are sometimes discarded prior to being consumed. However, these studies merely demonstrate the inadequacy of relying exclusively on otoliths (see also Fig. 7), and are therefore not pertinent in the present study.

The improved resolution achieved by utilizing a wide array of structures can be illustrated by examining the prevalence of the above prey species in selected collections in which they constituted the dominant prey. For example, herring elements were identified in 86.4–100% of samples ($\bar{X}$=96.1%; 150 of 156 samples) in 5 selected collections in which they were the dominant prey; and salmonids in 73.8–90.0% of samples ($\bar{X}$=77.7%; 73 of 94 samples) in 5 selected collections in which they were the dominant prey. The slightly lower prevalence of salmonids was probably due to the fact they were not consumed by all seals as most of the samples without salmonids contained other prey species. Nevertheless, even if it were assumed that all seals had consumed these prey, the prevalence of herring in the diet would only have been underestimated by a factor of 1.04, and the prevalence of salmonids by a factor of 1.29. In contrast, in the same collections herring otoliths occurred in only 62.7% of the samples containing herring and salmonid otoliths in only 9.6% of the samples containing salmonids. Thus, the prevalence of herring would have been underestimated by a factor of 1.59 and salmonids by a factor of 10.42 had only otoliths been used to identify prey.

The assertion that scat samples provided an accurate representation of diets is further substantiated

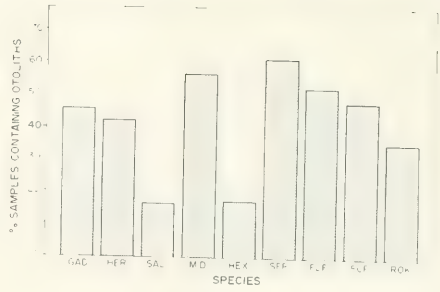

Figure 7

Percentage of scat samples in which various fish prey were represented by otoliths. Prey codes: GAD=gadoids; HER=herring; SAL=salmonids; MID=plainfin midshipman; HEX=hexagrammids; SFP=surfperches; FLF=flatfish; SCP=sculpins; and ROK=rockfish.

by the similarity of the prey identified in scat samples and those identified in stomachs collected within and adjacent to the study area. All but one of the 19 prey types identified in 69 stomachs collected throughout British Columbia (Fisher, 1952; Spalding, 1964) were represented in the scats, and all but 2 of the 22 prey types identified in 81 stomachs collected in Washington State (Scheffer and Sperry, 1931; Scheffer and Slipp, 1944). The exceptions were sablefish and ratfish, each of which occurred in one stomach, and burrowing crayfishes, which occurred in three stomachs. Furthermore, the mean number of prey species identified in the scat and stomach samples was also similar ($\bar{X}$=1.91 in scats versus 2.06 in stomachs).

Seasonal changes in diet composition outside of estuaries are shown in Figure 8A. Salmonids composed a relatively minor portion (0–5.2%; $\bar{X}$=3.1%) of the diet in all months. The diet was dominated by gadoids ($\bar{X}$=45.7%; 94.5% of which were hake) and herring ($\bar{X}$=33.0%). There was a pronounced seasonal shift between these two prey, with gadoids dominating during April–October (54.3–73.7%) and herring during December–March (58.0–70.2%). Other important prey, defined as those constituting ≥1% of the overall diet or ≥2% of the diet in any month, were hexagrammids ($\bar{X}$=3.4%; 95.8% of which were lingcod and 4.2% greenling), especially during December–April; plainfin midshipman ($\bar{X}$=3.4%), especially during April–June and November–December; surfperches ($\bar{X}$=2.2%; 81.3% of which were shiner perch and 18.7% pile perch); cephalopods (2.1%); and sandlance (0.9%). Incidental prey included, in decreasing order, rockfish, flatfishes, sculpins, smelts, skates, gunnels, lamprey, pricklebacks, crabs, sticklebacks, clingfishes, eelpouts and sea urchins. Unidentified prey accounted for a mean of 2.0% of the total nonestuary diet.

Seasonal changes in diet composition within estuaries are shown in Figure 8B. Salmonids were consumed in all months ($\bar{X}$=10.3%), but were most prevalent during during September–January (14.5–21.2%). As was the case outside estuaries, the dominant prey in estuaries were gadoids ($\bar{X}$=42.9%; 94.2% of which were hake) and, to a lesser extent, herring ($\bar{X}$=27.3%). Gadoids dominate (39.2–53.9%) in all months except February–March, when herring were dominant (49.5–50.6%). However, the seasonal shift in the importance of these prey was not nearly as pronounced as it was outside estuaries. Other important prey included plainfin midshipman ($\bar{X}$=3.6%) especially during May–June (9.7–10.5%); surfperches ($\bar{X}$=3.6%; 91.9% of which were shiner perch), flatfishes ($\bar{X}$=2.8%), sculpins ($\bar{X}$=2.6%), all of which were most prevalent during August–September (5.4–6.1%, 5.0–6.3% and 7.8–7.9% respectively); and cephalopods ($\bar{X}$=2.3%), especially during November–March (2.9–5.5%). Other incidental prey were, in decreasing order, rockfishes, sandlance, stick-

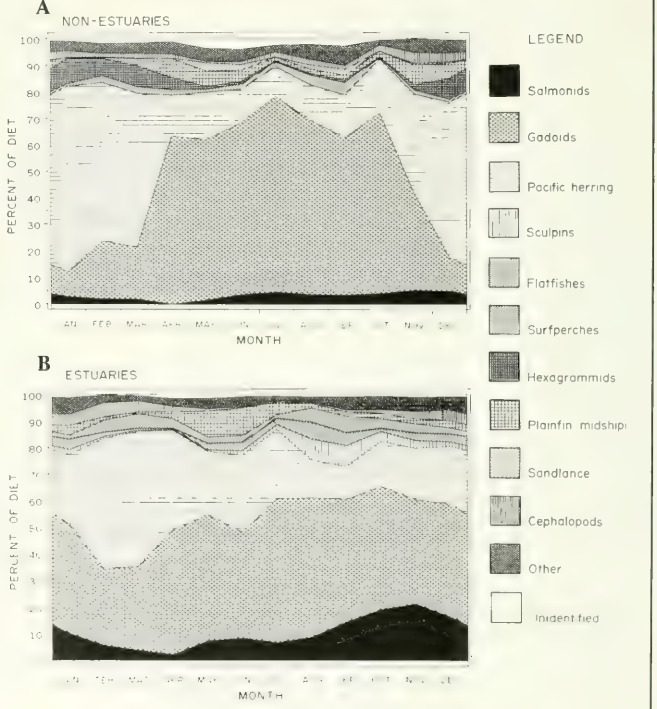

Figure 8

Seasonal changes in diet composition (**A**) outside of estuaries; and (**B**) within estuaries. Other prey include all those that constituted ≤2% of the diet in all months and ≤1% of the overall diet. Note that the patterns in the legend are ordered in the sequence they appear in the figures from bottom to top.

lebacks, hexagrammids, skates, northern anchovy, eelpouts, smelts, crabs, pricklebacks, gunnels, an unknown invertebrate, shrimp, lamprey, birds and mussels. Unidentified prey accounted for a mean of 1.0% of the overall diet within estuaries.

Estimates of the contribution of each prey to the total diet are shown in Figure 9, A–C. The estimates were obtained by integrating seasonal changes in distribution of seals (Fig. 3) with the seasonal changes in diet (Fig. 8), as per Equation 1. Although both the diet and abundance of seals varied regionally outside estuaries and among individual estuaries (see Olesiuk et al., 1990b for details), further stratification of the abundance and diet data by region and by individual estuary yielded estimates very similar to those shown in Figure 9, both in absolute terms (r^2=0.996 on an arithmetic scale) and in relative terms (r^2=0.879 on a log-log scale). The similarity can be explained by the fact that the scat samples were collected from all but one of 12 inhabited estuaries, from 47 widely distributed non-estuary sites and in all months of the year, and were thus representative of the entire population.

It was not possible to establish the absolute volumes of prey consumed from scats because the samples often represented only a portion of whole scats. Moreover, the relative volume of each prey consumed in a meal could not be reconstructed from the number and size of otoliths recovered and otolith length—fish weight keys (McConnell et al., 1984; Prime and Hammond, 1987; Harvey, 1989) because otolith recovery rates varied widely among species (Fig. 7) and intra-specifically depending on the size of prey (Olesiuk et al., 1990b). Furthermore, analogous analyses could not be applied to the other structures used to identify prey because their recovery rates also differed both among and within species (i.e., structures were recovered in proportions different from that in which they occur in whole prey). However, the lower and upper limits of the importance of prey in the diet, irrespective of the relative volumes of each prey consumed in meals, (see Table 3) indicate that estimates were fairly robust to violations of the equal-volume assumption. For example, the lower limits indicated that gadoids and herring combined accounted for no less than about half (47.8%) the overall diet. Indeed, subsequent calculations indicated that the two prey accounted for at least 63.2% of the total diet, because in many cases they were the only two prey species in a meal such that both could not have been consumed in negligible quantities. Upper limits for the remaining prey species indicated that none accounted for more than 10% of overall diet, and that only five families (salmonids, batrachoids, hexagrammids, embiotocids, and cephalopods) could have accounted for more than 5% of the overall diet.

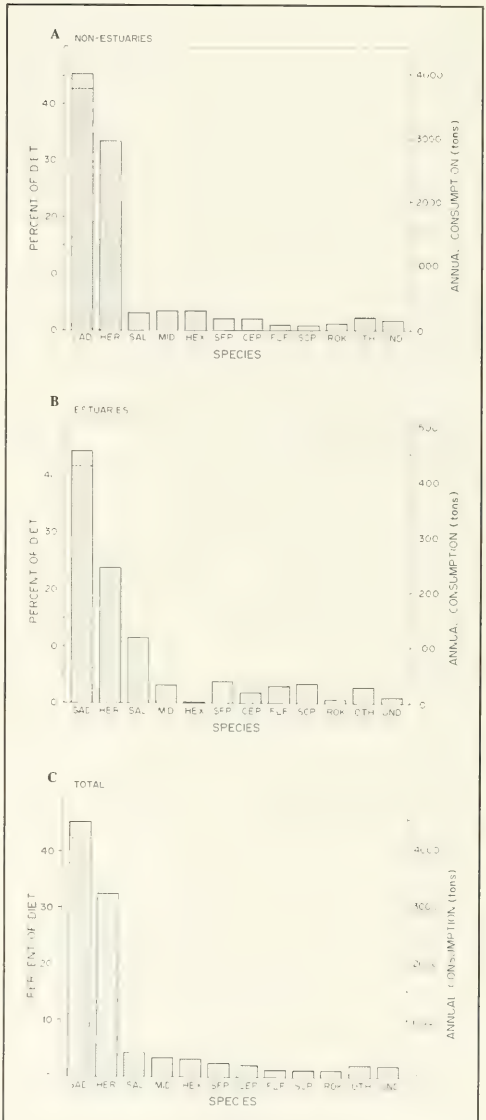

Figure 9

Contribution of prey to the overall diet (left scale) and estimated annual consumption (right scale) of important prey: (**A**) outside of estuaries; (**B**) within estuaries; and (**C**) for the entire study area. Prey codes: GAD=gadoids; HER=herring; SAL=salmonids; MID=plainfin midshipman; HEX=hexagrammids; SFP=surfperches; CEP=cephalopods; FLF=flatfishes; SCP=sculpins; ROK=rockfishes; OTH=other prey; and UND=unidentified prey. Dashed lines partition gadoids into hake (bottom) and all other species combined (top).

Prey consumption

Total annual prey consumption in the Strait of Georgia in 1988 was estimated at 9,892 metric tons (t) (range 6,432–13,359 t; Table 3), of which 1,023 t (range 665–1,381 t) was consumed within estuaries and 8,869 t (range 5,766–11,975 t) outside of estuaries. In energetic terms, this represented 65.8 TJ (6.8 TJ within estuaries and 59.0 TJ outside estuaries). The rate of energy consumption by the population was thus about 2.1 MW.

As noted earlier, most of the gross energy consumed was expended on maintenance and little on production. The ecological efficiency of the population was therefore low. Efficiency can be expressed either as the gross efficiency, which is the ratio of the gross energy consumed to energy added to the system through both mortality and surplus production (i.e., the 12.5% annual finite rate of increase), or as net efficiency, which includes only surplus production (i.e., net efficiency would be zero for a stationary population). In calculating energetic efficiency, the mean energetic density of carcasses was assumed to be 15.9 $KJ \cdot kg^{-1}$ based on a body composition of 30% blubber (37.8 $MJ \cdot kg^{-1}$) and 70% proteinaceous tissue (6.5 $MJ \cdot kg^{-1}$). In energetic terms, the gross population efficiency was estimated to be 3.9% and net efficiency to be 2.2%. The former estimate is consistent with the gross energetic efficiencies of 2.8% estimated for harbor seals in the Bering Sea (Ashwell-Erickson and Elsner, 1981), as well as the 3.8% and 3.9% for ringed and harp seals respectively (Parsons, 1977; Lavigne et al., 1982) and the 2–5% gross efficiency typical of mammals in general (Steele, 1974, cited in Lavigne et al., 1982). In terms of biomass, gross efficiency was estimated to be 1.6% and net efficiency 0.9%, which is also consistent with the gross estimate of 1.6% for harbor seals in eastern Canada (Boulva, 1973).

Gadoids (94% of which were hake both within and outside estuaries) accounted for the largest proportion of annual biomass consumed in the Strait of Georgia in 1988 (Table 3). Annual gadoid consumption was estimated at 4,467 t (454 t within and 4,013 outside of estuaries). Herring constituted the second largest proportion of the diet. Annual herring consumption was estimated at 3,206 t (244 t within and 2,962 t outside of estuaries). Salmonids ranked third in importance within estuaries and fifth outside of estuaries, and third overall. Annual salmonid consumption was estimated at 398 t (117 t within and 280 t outside of estuaries). Plainfin midshipman, which ranked sixth within estuaries and fourth outside estuaries, ranked fourth overall with an estimated 34 and 302 t consumed within and outside of estuaries respectively. Although hexagrammids constituted a negligible portion of the diet within estuaries, they ranked third outside of estuaries and thus fifth overall. Annual hexagrammid consumption was estimated at 311 t, 308 t of which was consumed outside estuaries. Other prey consumed in appreciable quantities (i.e., >100 t) included surfperches (23 t), cephalopods (20 t), flatfish (123 t), sculpins (114 t) and rockfishes (112 t). Annual consumption of all other prey combined, none of which composed ≥1% of the overall diet, was estimated at 208 t, and total consumption of unidentified prey at 181 t.

From the seal's perspective, approximately 44.2% (29.1 TJ) of the total annual energy requirements were obtained from herring and 33.3% (21.9 TJ) from hake. Thus, even though a larger biomass of hake than herring was consumed, hake were energetically less important than herring owing to their lower energetic density. Salmonids accounted for 3.3 TJ, which represented 5.1% of the total energy consumed compared to 4.0% of the biomass consumed. The precise energetic importance of other important prey could not be directly ascertained because their energetic densities were not known.

General discussion

Although formal statistical analyses are not possible with the available data, the model provides some insight into the likely accuracy of the annual prey consumption estimates. One potential source of bias in the consumption estimates are errors in the estimated daily energy requirements. Since the gross energy required for growth and reproduction constituted only a small portion of the overall population energy budget (1.7% and 4.5% respectively), uncertainties in these parameters, unless grossly underestimated, are unlikely to have an appreciable effect on the overall energy budget. Moreover, a large body of evidence indicates that the basal metabolic rates of adult phocids conform with Kleiber's (1975) equation (Lavigne et al., 1986). Thus, the two major potential sources of bias are the extent to which juvenile metabolic rates are elevated relative to adults, and the costs associated with activity. With respect to the former, the estimates of juvenile maintenance requirements based on captive seals and stomach contents of free-ranging seals differed by about ±20% of their mean. Because the study population was increasing at its intrinsic rate, it was markedly skewed toward juvenile age-classes which accounted for 62% of the total population energy budget. Hence, the discrepancy between the captive and stomach content estimates introduced a potential error of ±12% in the overall population energy budget. With respect to activity, the requirements of free-ranging seals probably fall somewhere between

those of captive seals and seals that swim continuously for 60% of the time. Since the latter two estimates differed from their mean by ±13% for all sex- and age-classes, the overall uncertainty in the estimated mean daily *per capita* energy daily requirements was probably on the order of ±25% of the point estimate.

Additional inaccuracies may be introduced in the conversion between units of energy and units of biomass due to seasonal, year-to-year, and age-related fluctuations in the energetic density of prey. For example, the energetic density of herring in the study area varies seasonally from 7.6 to 10.4 $MJ \cdot kg^{-1}$ (Bigg and Olesiuk, unpubl. data), a range of ±20% of the mean. However, because the seasonal fluctuations in herring are probably more pronounced than other prey, and because median energetic values of prey were adopted in the analysis, the typical potential bias is more likely on the order of ±10%. Since the potential biases in the energetic densities of prey and energy requirements are independent and additive, the total annual prey consumption estimate can be considered accurate to within about ±35% of the point estimate.

Further errors may be introduced in partitioning the total prey consumption among the different prey species. The main potential source of bias is the underlying assumption that all prey comprising a meal had been consumed in equal quantities. The lower and upper limits of the potential magnitude of this bias tended to be narrower for the two dominant prey (62–135% and 61–169% of the point estimates for hake and herring, respectively) than for other important prey, which averaged 35–211% of the point estimates. However, since it is very unlikely that a particular prey species was always consumed in negligible quantities or always comprised the entire meal when it was consumed along with other prey, these extreme limits undoubtedly overestimate the actual range of importance of prey. For example, when applied to the frequency of various fishes in 10,699 northern fur seal stomachs, the split-sample index actually gave results very similar to volumetric analyses (r^2=0.929 by region and r^2=0.978 overall with slopes and intercepts not significantly different from one and zero respectively) (Olesiuk et al., 1990b). If it is assumed that realistic lower and upper limits were half the width of the extreme limits, the total potential error in the estimates of annual consumption of hake and herring would be on the order of 50–170% of the point estimates, and 45–220% of the point estimates for other important prey species (see Table 3). It should be noted, however, that because the potential sources of bias in the consumption estimates are largely independent, the errors are just as likely to cancel as they are to compound.

The sex and age-structure of the population, which varies with the status of populations, had a surprisingly small effect on the mean *per capita* prey requirement. In the study population, which represented a population with a stable sex-and age-structure that was increasing at its intrinsic rate of 12.5% per annum, mean daily *per capita* food requirements were 1.9 kg, or 4.3% of mean body mass. If stationarity is induced by reducing fecundity rates, the parameter with the greatest influence on *per capita* requirements, the mean daily *per capita* requirement would increase to 2.1 kg, but decline to 3.9% of mean body mass. This is because the stationary population would be skewed more toward adults which not only have higher daily requirements, but also greater body masses. Thus, as also concluded by Lavigne et al. (1985) for harp seals in the northwest Atlantic, the population energy budget was relatively robust to direct changes in sex- and age-structure. In contrast, Hilby and Harwood (1985) found that energy requirements of grey seals were very sensitive to demographic changes. Their anomalous findings can be attributed to the fact that individual energetic requirements were scaled linearly to mass rather than $mass^{0.75}$, and also because the metabolic rates of juveniles were only marginally elevated (13%) relative to those of adults of equivalent mass. It should also be noted that populations may also experience density-dependent effects not directly related to demographic changes. For example, foraging costs may increase as prey become scarce, or seals may switch to alternate prey that would presumably have a lower energetic density or require greater energy expenditure to capture. These indirect effects were outside the scope of the basic model and could therefore not be evaluated.

Contrary to the assumption that thermoregulatory costs were negligible, some investigators have found that the metabolic rates of captive seals increased when immersed in colder water. Brodie and Pasche (1982) reported that resting metabolic rates of fasting grey seal pups increased in cold water as they depleted their blubber reserves, and on this basis suggested that *per capita* food requirements would increase in a population as prey became less abundant and the condition of animals declined. Hart and Irving (1959) found that the critical lower temperature of harbor seals in water was 20°C in summer and 13°C in winter, well above the ambient surface sea temperatures in the study area. However, because these experiments were conducted under artificial conditions, it is doubtful that the results can be validly extrapolated to free-ranging seals. For example, Figure 1 in Hart and Irving (1959) indicates that at 0°C, the resting metabolic rates of harbor seals were 1.4–1.8× greater than those within

the thermoneutral zone. However, the seals employed in their tests were restrained and probably post-absorptive. Even if it were assumed that basal requirements, which account for an average of 43% of the total energy requirements, were elevated to this extent for the 60% of the time seals spent in the water, thermoregulatory costs would only be on the order of 18–36 W. However, for a free-ranging seal, 17% of the GE ingested would be liberated as the heat increment associated with feeding and, since musculature is only about 25% efficient (Luecke et al., 1975), the remaining 75% of the 23% of GE expended for swimming would be liberated as heat. Since this "wasted" heat amounts to about 59 W for an average seal, it would appear that the thermoregulatory needs of free-ranging seals would be met indirectly through other energy expenditures.

One important assumption underlying the model was that daily ingestion rates were constant both with season and between regions. In contrast to other phocids such as harp and ringed seals (McLaren, 1958; Sergeant, 1973), Boulva and McLaren (1979) found no discernible seasonal pattern in the percentage of empty harbor seal stomachs, which implies that harbor seal feed throughout the year. As have previous models, the bioenergetics model assumed that feeding rates were constant in terms of biomass. Alternatively, it is possible that seals alter their foraging patterns in relation to the energetic density of prey. For example, greater quantities of poor-quality prey such as hake may be consumed when they are readily available compared to high-quality prey such as herring. Because any differences between the amount of energy ingested and required would be reflected by changes in energy reserves, the magnitude of potential biases introduced by these effects can be assessed from the seasonal changes in the condition of animals. Pitcher (1986) reported that the blubber composition of individual harbor seals ranged between extremes of 21% and 55% of body mass. Even if it assumed that the mean blubber content declined from 55% to 21% during a 6-month period of reduced food intake (or consumption of poorer quality prey) and increased from 21% to 55% during a second 6-month period of increased food intake (or consumption of higher quality prey), daily food requirements during the first and second 6-month periods would be only 125% and 75% of the annual mean respectively. Thus, gradual seasonal changes in food ingestion rates would not have a major effect on the prey consumption estimates.

Boulva and McLaren (1979) noted that the condition (i.e., girth:length ratio) of harbor seals of all ages and sexes combined was highest in winter and early spring, decreased during late spring, and was lowest in summer and late autumn. Similarly, Pitcher (1986) found that the blubber layer of adult males and females harbor seals were thickest in winter, thinned during the summer, and that females had even thinner blubber layers by the autumn moult. These observations are consistent, at least qualitatively, with my bioenergetics model which predicts that animals would accumulate blubber during the winter while feeding mainly on energy-rich herring and deplete blubber during the summer while feeding mainly on energy-poor hake. The model also predicts that nursing females would utilize an additional 16.8 kg of blubber, or 22% of their total body mass, during the late July to early September nursing period (Bigg, 1969), and would therefore be in poorer condition than males by the autumn moult.

In an earlier assessment for harbor seals in the Bering Sea, Ashwell-Erickson and Elsner (1981) estimated the mean daily *per capita* gross energy requirements to be 216–238 watts, which is 26–38% greater than my estimate of 172 watts. The difference appears to be almost entirely attributable to geographic differences in body size. The mean body mass of harbor seals (both sexes were combined) in the Bering Sea was 67.7 kg, which is about 50% greater than the mean body mass of 44.7 kg in British Columbia. This difference translates into about a 37% difference in metabolic mass ($M^{0.75}$), to which energy expenditures were scaled in both our models.

After my model had been completed, Harkonen and Heide-Jorgensen (1991) published a very similar model for harbor seals in the Skagerrak. There is good agreement between our models on how the energy budget is partitioned among various components. Harkonen and Heide-Jorgensen (1991) estimated that, for an increasing population, 73.1% of metabolizable energy (NE and the heat increment) is expended on maintenance, 19.0% on activity, 2.0% on growth, 4.5% on reproduction, and 1.5% on the annual moult. According to my model, 68.1% is expended on maintenance (including the heat increment), 26.9% on activity, 1.4% on growth, 3.7% on reproduction, and I made no allowance for any costs associated with the annual moult. However, there is a considerable discrepancy between our estimates of the mean daily *per capita* gross energy requirements, even though the mean body mass of seals in the Skagerrak and British Columbia are very similar (41.8 and 44.7 kg respectively). Harkonen and Heide-Jorgensen's (1991) estimate of 227 watts is 32% greater than my estimate of 172 watts. This discrepancy is due primarily to differences in the way energetic requirements were scaled to body mass. Harkonen and Heide-Jorgensen (1991) first estimated the requirements of juveniles and then extrapolated these estimates to adults by assuming

that energy expenditures were linearly related to body mass (their correction of 1.4 to account for non-mass related differences between juveniles and adults was almost identical to mine). In contrast, energy expenditures in my model were scaled according to metabolic mass ($M^{0.75}$), which increases less rapidly with age than body mass. According to my growth curves, the increase in body mass between weaning and adulthood would be 29% greater than the increase in metabolic mass over the same period for females, and 39% greater for males.

Despite the aforementioned limitations, my bioenergetics model provides some insight into the foraging patterns of harbor seals in the Strait of Georgia. Hake and herring, the two most abundant fishes in the study area (Shaw et al., 1990; Hay et al., 1989), are clearly also the two most important prey of harbor seals. Combined, they account for an estimated 75% (at minimum 63%) of the total consumption both in terms of biomass and energy. One would therefore expect hake and herring stocks to play an important role in regulating the size of the harbor seal population, if in fact carrying capacity is food-limited. The annual consumption of these prey by harbor seal population in 1988, which is thought to be near or perhaps slightly above historic levels (Olesiuk[4]), represents approximately 3.2% of the total hake biomass in the study area (Shaw et al., 1990) and 3.5% of the total herring biomass (Haist et al. 1988; Hay[10]).

Interestingly, both hake and herring appear to be only seasonally available in the Strait of Georgia, but in a reciprocal manner to one another. The Strait of Georgia of herring stock is largely migratory. Adult herring normally reside off the west coast of Vancouver Island, but emmigrate into the Strait of Georgia during December–March to spawn (Taylor, 1964; Hay et al., 1987; Hay et al., 1989). Although the Strait of Georgia hake stock is resident, hake are scarce throughout much of the Strait during December, and by March have congregated in deep (150–300 m) spawning aggregations in offshore waters. Following spawning, the spawning aggregations disperse and during April–November hake occur in shallower waters (50–100 m) throughout much of the Strait of Georgia (McFarlane and Beamish, 1985), which coincides with the period herring are unavailable. Thus, hake and herring provide an abundant year-round source of food, as reflected by the seasonal shift in the predominance of these prey in the diet (Fig. 8A). The year-round availability of these two abundant prey may account for the much higher density of seals in the study area compared to other regions of British Columbia (Olesiuk et al., 1990a).

Seasonal fluctuations in the overall importance of hake and herring were much less pronounced in estuaries (Fig. 8B). In some estuaries the seasonal shift between these two prey were similar to those outside estuaries, whereas in other estuaries hake dominated the diet in all months (see Olesiuk et al., 1990b for details). Seals in the latter estuaries were probably feeding on small, localized stocks that are non-migratory and are known to reside nearby[11], or on juvenile hake which move inshore and inhabit shallow waters (McFarlane and Beamish, 1985).

Although hake and herring represented the major food items, a wide array of other species were consumed in small quantities. Predation on these prey appeared to be largely limited to the particular areas and periods each was most available or vulnerable. For example, adult salmon were consumed primarily as they concentrated en route to spawning rivers, and especially within estuaries. Numbers of seals in most estuaries also increased during September–December coinciding with the return of spawning salmon to adjacent rivers (Olesiuk et al., 1990b). Plainfin midshipman and lingcod were also preyed upon primarily during their spawning seasons when males defend nests, and trout in a few localities as they were released in large quantities from hatcheries or returning to spawn in natal rivers (Olesiuk et al., 1990b). Since these prey comprised a minor component of the overall diet, they probably play little role in regulating harbor seal abundance.

This study indicates that the harbor seal is an opportunistic predator in that it is capable of adjusting its foraging patterns to take advantage of seasonally and locally abundant or vulnerable prey. Although the low efficiency of the population may be construed as reinforcing the premise that seals are "inefficient converters of fish flesh" (Sergeant, 1973), the ecological efficiency of harbor seals is actually comparable to that of many terrestrial mammals (see review in Lavigne et al., 1982) and slightly above the theoretical upper limit of 2–3% expected for homeotherms (Turner, 1970). In order to acquire a more complete understanding of the role of harbor seals in the ecosystem, it will be necessary to extend the bioenergetics model to the community level (Lavigne et al., 1982). The population model raises several complex questions that can only be answered by community models. For example, to what extent is the sex- and age-structure and productivity of herring stocks affected by harbor seal

[10]D. Hay, Pacific Biological Station, Nanaimo, B.C., pers. commun. 1989.

[11]G. McFarlane, Pacific Biological Station, Nanaimo, B. C., pers. commun. 1989.

predation; or to what degree are the overall predatory pressures on herring affected indirectly by seal predation on other herring predators such as hake, salmon, and lingcod? Such a bioenergetics community model will need to incorporate not only data on the size of prey consumed, which can be obtained from a more detailed analysis of scat contents (e.g., Bailey and Ainley, 1982; Antonelis et al., 1983), but also the dynamics and compensatory and depensatory mechanisms of population regulation of prey populations.

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Abstract.—Habitat association, growth, and burrowing behavior were examined for a population of young-of-the-year juvenile queen conch, *Strombus gigas* L., in the southern Exuma Cays, Bahamas, during the winter 1988–1989. These early juveniles (35–54 mm siphonal shell length) primarily inhabit shallow unvegetated zones where they burrow in the sediment during the day and surface at night. Laboratory experiments showed that the burrowing rhthym was endogenous. Highest densities of 1- and 2-year-old juveniles (80–140 mm) conch were observed in adjacent, deeper seagrass beds, suggesting that queen conch make an ontogenetic shift in habitat. Results of an enclosure experiment revealed that growth rates of early juvenile conch were higher in seagrass (0.11 mm/day) and in rubble (0.09 mm/day) than in bare sand (0.01 mm/day) where they were initially found. These observations suggest that emergence of juvenile conch and movement to vegetated habitats at 35–54 mm shell length is associated with changes in nutritional requirements. Changing habitat association with age may also be related to predator avoidance and burrowing capabilities. Habitat requirements of early juvenile conch are different from those of 1-year-old juveniles and stock enhancement programs will need to consider ontogenetic habitat shifts.

Ontogenetic shift in habitat by early juvenile queen conch, *Strombus gigas*: patterns and potential mechanisms

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Declining populations of queen conch (*Strombus gigas* L.), usually attributed to overfishing, have been reported for numerous areas in the Caribbean region (Brownell and Stevely, 1981; Appeldoorn et al., 1987; Berg and Olsen, 1989). Hatchery production and field release of juvenile conch have been suggested as a means of restoring depleted stocks (Berg, 1976; Brownell, 1977; Davis and Hesse, 1983; Iversen et al., 1986) but release methods have not been perfected (Stoner, unpubl. data). Although survival in small juvenile conch is low in natural populations (Appeldoorn, 1984), mass rearing of large juveniles (1- and 2-years-old) is costly (Siddall, 1983) and releases will need to be made with 0+ year class conch. Unfortunately, pilot releases of small conch have resulted in very low survival (Appeldoorn and Ballantine, 1983; Siddall, 1983; Appeldoorn, 1985), probably because of the lack of ecological information on early stage juveniles and problems associated with the identification of suitable habitats (Iversen et al., 1986; Stoner and Sandt, 1991; Stoner, unpubl. data).

Despite high densities (1–2/m^2) of 1- and 2-year old conch (80–140 mm shell length) in certain seagrass meadows (Alcolado, 1976; Weil and Laughlin, 1984; Stoner and Waite, 1990; Wicklund et al., 1991; Stoner et al., 1993), individuals less than 50–60 mm in shell length (called early juveniles in this study) have rarely been seen in the field. Iversen et al. (1986) suggested that these early juvenile conch probably spend a large part of their time buried in the sediment. Attempts have been made to find them using suction dredges (Iversen et al., 1987; Stoner, unpubl. data) but few early juveniles have been collected and, to date, no quantitative data exist.

An opportunity to gather information on the distributional ecology and behavior of early juvenile queen conch was provided by the fortuitous discovery of a 0+ year class population near Neighbor Cay, in the central Bahamas, in January 1989. The subsequent investigation was designed: 1) to quantify habitat-specific distribution and abundance patterns, 2) to examine habitat-specific growth rates, and 3) to examine burrowing behavior in relation to time of day and light cues. The findings are discussed in terms of stock rehabilitation and management.

Study site

The distribution and behavior of early juvenile queen conch was investigated near the north shore of

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Neighbor Cay in the southern Exuma Cays, Bahamas (28°48.84'N, 76°11.9'W) (Fig. 1). The study site was located between a section of shoreline beachrock and subtidal carbonate rubble to the east and a sand bar to the west which extended outward from the shoreline (Fig. 2). Tidal currents ran parallel to shore and increased from near zero at the shoreline to 50 cm/s or greater 200 m from shore. The tidal range was 1.0 m.

Distribution and abundance of conch was examined along a 110-m section of nearshore shallow habitat (0–1.9 m deep at mean low water). Several zones extending to 25 m offshore from the low water mark were identified (Fig. 2). Zone A was intertidal, between high and low water marks. Zone B consisted of the shallowest subtidal area extending from shore to the top of a steep surf berm (zone C). Zone D was a sparsely vegetated transition area between either zone C (stations 1–7) or zone B (stations 8–12), and zone E. Zones A through C were bare sand habitats. Zones E, F, and G were areas vegetated with turtlegrass, *Thalassia testudinum* Konig and small amounts of shoal grass, *Halodule wrightii* Konig (Table 1). Measurements and experiments in zone E were made 2.5 m from the inshore edge of the seagrass (Fig. 2). Measurements in Zones F and G were made 10 and 20 m, respectively, from the seagrass edge. The rocky area to the east was a carbonate cobble covered with macroalgae including an abundant turf of the green algae *Cladophoropsis membranacea* and *Batophora oerstedi*, along with clumps of the branched red algae *Laurencia obtusa*, *L. poitei*, and *Graciolaria compressa*. The adjacent seagrass area (zones E, F, G) is a known, long-term (>5 years) nursery habitat for queen conch (>1-yr-old) studied earlier by Stoner and Sandt (1991).

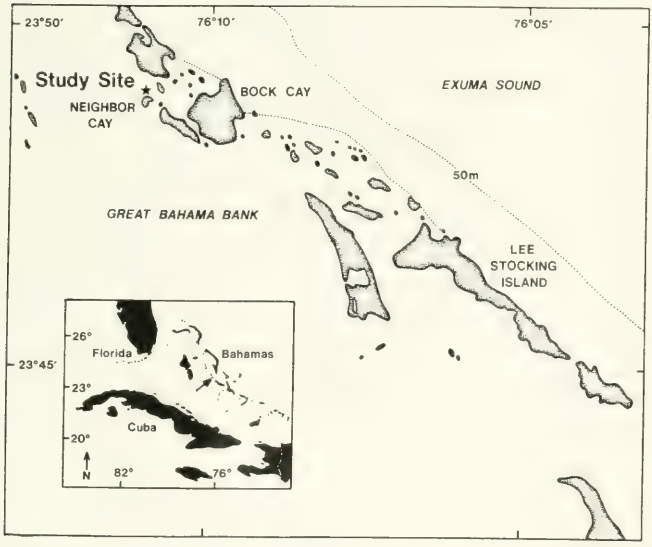

Figure 1

Map of the Lee Stocking Island area in the central Bahamas, showing the location of the Neighbor Cay study site where early juvenile queen conch were found.

Methods and material

Environmental measurements

Sediment grain-size and organic content, two factors frequently important in the distribution of infaunal animals, were measured in each zone (A to G) and along each transect perpendicular to the beach where possible (Fig. 2). Sediments to 5.0 cm depth were collected in a 40-mm diameter core and frozen (–15°C) until analysis. In the laboratory, one thawed sediment subsample of approximately 100 g wet weight was dried for at least 24 hours in an oven at 80°C to constant weight and incinerated at 550°C in a muffle furnace for 4 hours. Organic content was estimated as the percent difference between dry weight and ash-free dry weight. A second sediment subsample of approximately 50 g was used to measure granulometric properties. Grain-size for the sand fraction was determined by using standard sieve procedures (Folk, 1966), after removing salts and extracting the silt-clay fraction by washing with freshwater on a 62-μm mesh screen. Silt-clay fractions were analysed with a standard pipet procedure (Galehouse, 1971). Product moment statistics were generated for mean grain-size (McBride, 1971).

Relative cohesiveness of the sediment was measured in the field at every non-rocky station by using a 50-cm-long steel rod (15.3 mm diameter) equipped with a sliding lead weight (1.3 kg) and a stop 17 cm above the end of the device. The rod was placed vertically on the surface of the sediment, the weight was raised 25 cm on the steel shaft and dropped. Penetration was measured in mm, and the average of two measurements was recorded.

Seagrasses, macroscopic detritus (identified as being mostly senescent seagrass blades), and macroalgae were collected on transects 3, 5, 7, and 9 in the 3 vegetated zones E, F, and G. Samples were collected from a 25 × 25 cm quadrat into 3-mm mesh bags. Detritus and

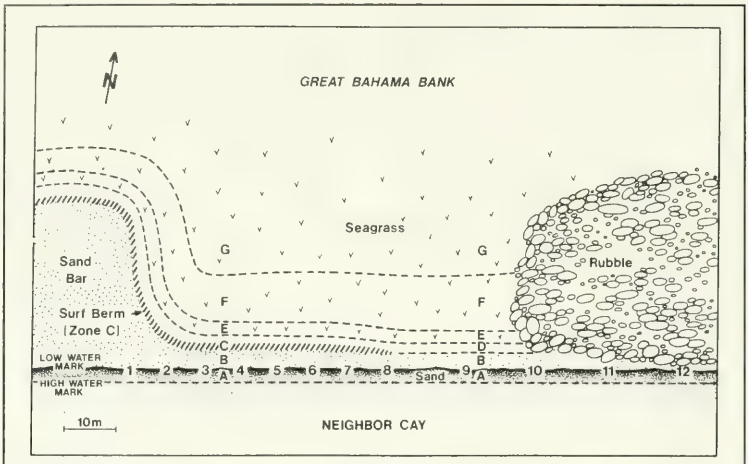

Figure 2

Detailed map of the Neighbor Cay, Bahamas, study site showing the habitat zones where environmental measurements and conch density were made. Zones A, B, C, and D are bare sand. Zones E, F, and G are vegetated with turtlegrass (*Thalassia testudinum*). Numbers at the mean low water line (MLW) indicate positions of transects which ran perpendicular to the beach.

above-ground parts of the macrophytes were separated by species and dried at 80°C for 24 hours. The individual components were weighed (0.1 g) and biomass was expressed in g dry weight/m^2. Water depth was measured at mean low water at every station in each zone.

Conch distribution

Conch density (no./m^2) was determined in January 1989 at each station by searching two 0.75-m radius circles (to 10 cm depth) to extract buried conch. Preliminary observations at the Neighbor Cay study site showed that burial depth was limited to 3–4 cm for 35–54 mm conch. All conch were counted and measured for shell length (SL, spire to siphonal groove).

In early February 1989, heavy mortality due to predation reduced the early juvenile population by at least 50%. Crushed shells of small conch were abundant in all of the primary habitats, and crabs were the suspected predators. Few free-ranging, tagged conch were found alive after that time.

Table 1

Habitat characteristics in seven zones (A–G) surveyed for early juvenile conch at Neighbor Cay, Bahamas (see Fig. 2).[1] Values are mean ±SD and number of measurements for each zone are in parentheses.

	A	B	C	D	E	F	G
	(12)	(10)	(8)	(9)	(10)	(7)	(7)
Depth	–0.2 ± 0.1	0.3 ± 0.1	0.7 ± 0.2	1.3 ± 0.4	1.4 ± 0.5	1.6 ± 0.1	1.9 ± 0.1
Sediments							
Grain-size	984 ± 116	974 ± 187	796 ± 250	705 ± 204	521 ± 90	490 ± 64	496 ± 64
Organics	2.59 ± 0.36	2.60 ± 0.28	2.62 ± 0.32	2.74 ± 0.22	2.73 ± 0.5	2.68 ± 0.26	2.70 ± 0.22
Relative cohesiveness	48 ± 7	48 ± 13	127 ± 35	47 ± 9	41 ± 7	40 ± 3	43 ± 6
Macrophyte biomass							
Thalassia testudinum	0	0	0	0	11.4 ± 5.6	8.8 ± 3.7	12.5 ± 4.0
Halodule wrightii	0	0	0	0	0.1 ± 0.2	0.1 ± 0.1	0.2 ± 0.3
Macrodetritus	0	0	0	0	4.8 ± 0.8	1.1 ± 0.6	1.3 ± 1.4

[1]Units for each characteristic are: depth (m at mean low water: MLW) (negative depth is height above MLW), sediment grain size (μm), sediment organics (% of dry weight), relative cohesiveness (mm), *Thalassia*, *Halodule*, and macrodetritus biomass (g dry weight m^{-2}).

Enclosure experiment

Habitat-specific growth rates were examined experimentally in covered enclosures. Circular cages, 1.5 m in diameter (1.77 m^2) were constructed with polyethylene mesh (1 × 1 cm) wired to a reinforcement bar driven into the sediment. Two cages were built in zone B, near transect 6 in bare sand, two were placed in the seagrass zone E, and two were built in the rocky zone between transect 11 and 12 (Fig. 2). The mesh was pushed into the sediment approximately 5.0 cm to prevent escape of conch. Tops of the cages were covered with the same plastic mesh to exclude predators.

Conch between 37 and 49 mm SL were collected in zone B. After removing all visible invertebrates from the 6 cages, 8 individually tagged and measured conch were randomly assigned to each cage. This yielded a density of 4.5 conch/m^2, near the highest natural densities of similar size class conch in the field.

The experiment was initiated on 3 February 1989, examined after 19 and 41 days for cage damage and conch loss, and terminated after 63 days. Growth rates were expressed in mm shell length per day.

At the end of the enclosure experiment, conch were collected and frozen for measurement of body condition factor and stomach analysis. After thawing, the animals were drawn from their shells and rinsed to remove feces and mucus. All undamaged conch were blotted lightly and weighed (0.1 g). Condition factor was expressed as the ratio of soft tissue weight:shell length (g/mm). No significant sexual dimorphism occurs in queen conch until the gonads begin to develop at approximately 2 years of age; therefore, sex of the experimental animals was not considered.

Stomach contents, removed from the conch and preserved in a 70% solution of ethanol mixed with dilute rose bengal, were quantified by the gravimetric sieve-fractionation method of Carr and Adams (1972). Pooled contents from the stomachs of conch from each experimental treatment were washed through a series of four sieves of decreasing mesh size (425, 250, 150, and 75 µm, and each sieve fraction was examined under a dissecting microscope (20–40×). Food items were heavily macerated but easily classified into general taxonomic categories; these included algae, detritus, and small invertebrates such as foraminiferans, gastropods, and polychaetes. The proportion of each food type (as well as sand) in each sieve fraction was estimated by identifying and counting the individual particles. After examination and identification, each sieve fraction was dried for 12 hours at 80°C. Dry weights of the fractions were summed and the relative importance of the different food categories were reported as the percentage of total dry weight.

Analysis of variance was used to test the significance of differences in growth and condition factor among the habitat treatments. Because multiple measurements from individual enclosures are pseudoreplicates (Hurlbert, 1984), mean values from the replicate cages were used in the analyses. Growth rates were $\log_{10}$-transformed to produce homogeneity in variance (Box test, $F = 0.511$, $P = 0.608$). Transformation was unnecessary for condition data. Tukey's test was used for multiple comparisons.

Burrowing in the field

Early juvenile conch were first observed at Neighbor Cay late in the day (17:00 hours) on 8 January 1989, but none were visible the following morning. Assuming daytime burial, a survey of the population was initiated to examine diel periodicity in burrowing behavior. On 17 January, 64 early juveniles were tagged with vinyl orange spaghetti tags (Floy Tag & Manufacturing, Inc.) tied to the shell spire and released in zone B of the study site. A 4-cm free end was left on the tag so that buried conch could be easily seen and counted. During the survey, all early juvenile conch were tagged when observed (500 total).

Surveys for buried conch were made on 22 dates between 17 January and 28 February 1989. Between 17 January and 7 February, surveys were made by two divers swimming parallel to the beach. All tagged conch were counted and their behavior was recorded as either on the surface, or buried. Because massive mortality due to predation on early juveniles occurred during the first week of February, subsequent observations were made on the tagged conch held in experimental enclosures (see previous section). Over the course of the study the beach was surveyed at nearly all times of day and night and at different stages of the tide. Twice in January, surveys were made each half-hour during each of the transitions from dark to light and from light to dark. This permitted observations on the precise time of emergence and burrowing relative to times of twilight, sunrise, and sunset. Timing on 53 surveys was such that observations were made at least once or twice every half hour through day and night.

Burrowing in the laboratory

The role of light stimulus on burrowing behavior of early juvenile conch was examined by subjecting them to different light-dark cycles in laboratory aquaria. Because most of the early juveniles found in the field had been manipulated during previous experiments, we

used hatchery-reared conch (39–53 mm SL) as subjects for this experiment.

Nine 190-L aquaria containing 5 cm of coarse sand from Neighbor Cay (zone B) were used in the experiments. Water temperature was maintained at approximately 28°C, and aeration was provided by undergravel filters. Ten juvenile conch were placed in each of the aquaria and subjected to a schedule of 12 hours light:12 hours darkness. After 4 days, when the burrowing cycles of the animals became apparent, the animals were subjected to three different light regimes during the subsequent 4 days: three aquaria were kept under natural cycle (12:12), three were placed under continuous darkness and three under continuous light.

Observations on burrowing behavior were made twice during the day and twice during the night (0400, 1100, 1500, 0000 hours). Food, in the form of seagrass detritus, was placed on the surface of the sediment.

Results

Habitat characteristics

Transects from the intertidal beach to the shallow subtidal seagrass bed were characterized by increasing water depth ranging from –0.2 m (at MLW) in the center of intertidal zone A to 1.9 m in zone G. Sediment grain-size decreased with increasing depth (Table 1). In zones A through E sediments were coarse sands (984-521 μm), while medium sands (496-490 μm) were found in zones F and G. Organic content of the sediments varied little across the different zones, ranging from 2.59 to 2.74% of dry weight (Table 1). Sediment cohesiveness was relatively constant across the offshore zones (40–48 mm), except in the surf berm (zone C), where cohesiveness was low (i.e., penetrability and porosity were high) (Table 1).

Seagrasses, primarily *Thalassia testudinum*, were present in relatively low biomass in zones E, F, and G (Table 1). Dry weights of macrodetritus were also relatively low, with the highest mean value (4.8 g dry wt/m^2) observed in zone E.

Conch distribution

In the January survey, all conch found were less than 60 mm or greater than 80 mm SL. Given the summer spawning season of queen conch in the Exuma Cays (Stoner et al., 1992) and estimated growth, it was assumed that the former represented the young-of-the-year class (0+), while those larger than 80 mm were 1- and 2-year old conch. Eighty-six percent of the early juvenile conch (35–54 mm SL) were found in unvegetated zones B, C, and D (i.e., in the immediate subtidal, in the surf berm, and at the bottom of the slope, respectively). All others were found in the vegetated zone E (Fig. 3). No early juvenile conch were found in the most offshore zones F and G. Mean density of early juveniles (1.25 conch/m^2) was greatest in zone C, in association with the coarser grain sizes and low sediment cohesiveness (Table 1). In contrast to the narrow, high beach distribution of early juveniles, later stage juveniles were found in every zone, and highest densities in the seagrass zones E, F, and G (Fig. 3).

Most of the early juvenile conch were distributed between transects 3 and 9 (Fig. 2) over an area of approximately 250 m^2. Based on a mean density of 1.25 conch/m^2 in zone C and 4 conch/m^2 observed in some areas of zone C, the early juvenile population was between 275 and 1000 conch. The densities observed probably accounted for most of the total population since 500 conch were tagged during night observations.

Enclosure experiment

No mortality occurred during the first two periods of the transplant experiment; therefore, no replacements were necessary and growth rates were calculated for the original conch (Table 2). At the end of the experiment, two conch were found dead, one on sand and one on seagrass. Five conch were unaccounted for, two in the sand treatment, two in the rocky zone, and one in the seagrass habitat.

Growth rate in the sand habitat was much lower (0.012 mm/day) than the rates in seagrass (0.112 mm/day) and rock habitats (0.094 mm/day) (Table 2). The differences were significant (ANOVA, F = 769.35,

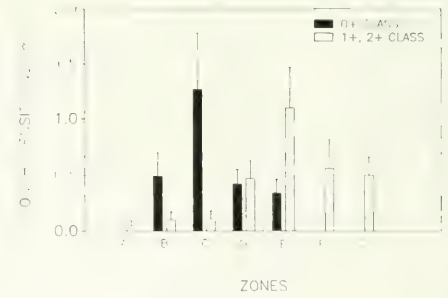

Figure 3
Density of queen conch juveniles at Neighbor Cay, Bahamas, shown as a function of habitat zone (see Fig. 2). The 0+ year class comprises conch <60mm shell length. The >0+ category includes all juvenile conch >80mm. Values are mean +SD.

Table 2

Daily growth rate in shell length and body condition factor[1] of early juvenile conch (37–49 mm shell length) held in enclosures on sand, seagrass, and rock habitats. Values are means ±SD. Two enclosures with eight conch each were used in the analysis. Differences among treatments were different for both growth rate (ANOVA on log-transformed data, $F = 769.35$, $P < 0.001$) and condition factor (untransformed data, $F = 12.82$, $P = 0.034$). Letter codes indicate mean values which were not significantly different (Tukey's multiple comparison test, $P > 0.05$).

	Treatment		
	Sand habitat	Seagrass habitat	Rock habitat
Growth rate (mm/day)	0.012 ± 0.001[a]	0.112 ± 0.010[b]	0.094 ± 0.002[b]
Condition factor (g/mm)	0.027 ± 0.001[a]	0.042 ± 0.002[b]	0.039 ± 0.005[ab]

[1]Condition factor is defined as the wet weight of soft tissue divided by shell length of an individual.

$P < 0.001$), and Tukey's multiple range test indicated that conch in sand grew at a rate lower than those in seagrass and rock habitats ($P < 0.001$). Growth rates ($P = 0.124$) for conch in seagrass and rock were the same.

Condition factor was also lower in the sand treatment (0.027), than in seagrass (0.042) and rock habitats (0.039) (Table 2). The habitat effects were significant (ANOVA, $F = 12.82$, $P = 0.034$). Differences in mean condition factor in seagrass and sand treatments were significant (Tukey's test, $P = 0.035$), but the differences were not significant in sand and rock ($P = 0.063$) or seagrass and rock ($P = 0.648$).

Stomach contents of conch from the three different habitats were primarily algae and sand (Table 3). Conch enclosed in the rocky zone had a lower percentage of sand (26.5%) in their stomachs than conch in the other two habitats (48.6–58.2%); however, algae made up over 87% of the organic constituents of the stomach contents in all cases. Detritus particles, identified as *T. testudinum*, represented a small percentage of stomach contents of conch held in seagrass and rock habitats (Table 3). Foraminifera and Gastropoda found in the stomachs were small forms (<1 mm), probably taken incidentally with sand particles. The only polychaete found was *Spirorbis* sp., a small, sessile, tube-builder probably taken with epiphytic algae. Non-sand weight per stomach was highest for the conch in the rock habitat (Table 3).

Burrowing experiments

Fewer than 30% of the early juveniles observed in the field were found on the surface during the day, whereas almost 100% were found on the surface at night (Fig. 4). Detailed observations near crepuscular hours showed that conch buried themselves before sunrise and surfaced before sunset. There was no indication of tidal rhythm on burrowing during our study.

Juvenile conch demonstrated lower percentages of burrowing in the laboratory than in the wild; but a marked rhythm in burrowing was observed during the four days of acclimation (Fig. 5). After light manipulations began, conch exposed to natural cycles of light (12 hours:12 hours) continued to emerge from the sediment in darkness hours (Fig. 5). Conch held in constant darkness demonstrated a much reduced frequency of burying themselves but this pattern became more erratic by the end of the experiment. Conversely, animals held in constant light continued to show natural rhythms of activity (i.e., burying themselves and surfacing on the light-entrained schedule).

Discussion

Queen conch less than 50 mm SL have rarely been observed on the sediment surface. Iversen et al. (1986) concluded that conch spend their first year of life buried in the sediment, after which time they are prima-

Table 3

Stomach contents of early juvenile conch (38–55 mm shell length) from the enclosure experiment. Individual components are expressed as the percent of dry stomach contents weight. Number of conch sampled from each habitat are in parentheses.

	Treatment		
	Sand habitat (12)	Seagrass habitat (15)	Rock habitat (10)
Sand (% of total weight)	58.2	48.6	26.5
Food Items (% of food weight)			
Algae	87.9	91.9	96.1
Foraminifera	10.5	7.5	2.1
Gastropoda	0.5	0.4	0.6
Polychaeta	1.1	0.0	0.4
Detritus	0.0	0.2	0.8
Food Weight (mg/individual)	7.0	9.0	15.5

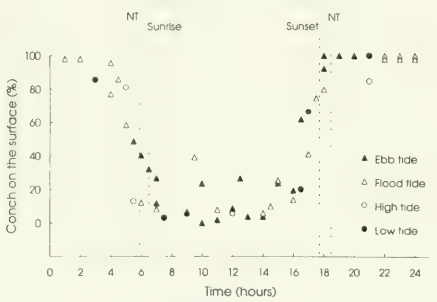

Figure 4

Percentage of early juvenile conch on the sediment surface at Neighbor Cay, Bahamas, at different times of day. Local time of nautical twilight (NT), sunrise, and sunset are shown. Observations were made between 17 January and 28 February 1989. State of tide is indicated for the individual times of observation.

rily epifaunal. Our observations of burrowing rhythms in 35–54 mm queen conch at Neighbor Cay corroborate Randall's (1964) conclusion that early juvenile queen conch emerge from the sediment at night, but the extent to which smaller conch remain buried is unclear. Because early juvenile conch were never observed between the summer spawning season and the January discovery of 35-mm conch, we hypothesized that burrowing progresses from full-time activity in conch less than approximately 25 or 30 mm until near continuous epifaunal existence in conch at approximately 1 year of age.

Early juvenile conch lack long spines and strong shells characteristic of older juveniles, and burrowing in shallow waters is probably a predator avoidance mechanism (Iversen et al., 1986, 1989). Laboratory experiments have shown that shell strength in queen conch increases rapidly with length above 55 mm (Jory and Iversen, 1988), similar to the size at which conch at Neighbor Cay became apparent on the sediment surface. Shell structure may also explain the typical age-specific type IV survival patterns observed in *Strombus gigas* and *S. costatus* (Appeldoorn, 1984). The significance of shell size and spination in providing protection from predators has been shown experimentally for other gastropods (Palmer, 1979).

Conch burrowing may also vary with age-related morphological constraints or with microhabitat features. For instance, burrowing abilities in queen conch may be reduced with increase in size and associated apical spination (Marshall, 1988). Also, low sediment cohesiveness probably facilitates burial. This may explain the high density of early juveniles in the surf berm at Neighbor Cay.

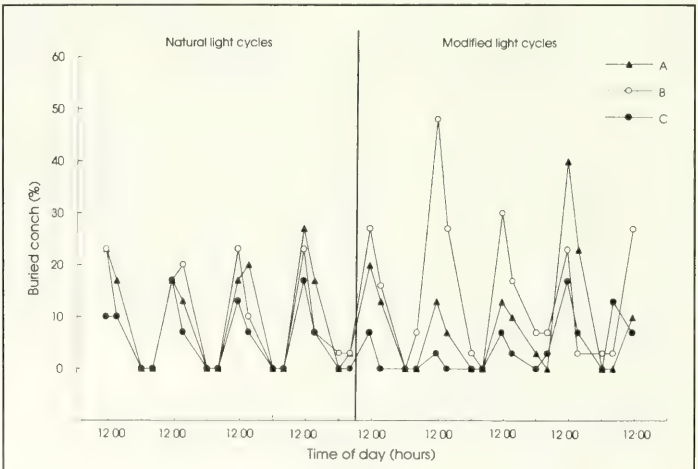

Figure 5

Frequency of burrowing in early juvenile queen conch held in the laboratory. Four days of natural light cycle (12 hours light:12 hours dark) were followed by 4-day periods of modified light cycle. The modified light treatments were A = continued natural light cycle, B = constant light, and C = constant dark. Values shown are the means for three separate runs (see text for explanation of methods).

Early juvenile conch were not present in seagrass zones where 1- and 2-year-old conch were most abundant; this observation suggests that the distribution pattern was related to an ontogenetic shift in habitat rather than differential survivorship. Conch between 35 and 54 mm probably moved from sand to vegetated habitats to exploit higher algal concentrations. Stomach analysis indicated that algae are the primary dietary components for early juvenile conch at Neighbor Cay, similar to the diets of older individuals (Stoner and Waite, 1991). In sandy substrates, these foods probably become limiting as conch grow in size and food intake. This conclusion is supported by the results of our enclosure experiment which showed low growth for 37–49 mm conch held in the sand habitat. Growth rates were much higher in seagrass (0.11 mm/day) and rocky habitats (0.09 mm/day) than in sand (0.01 mm/day), and were similar to the rate (0.09 mm/day) observed in an earlier study of 1-year-old juveniles enclosed in seagrass at the same site (Stoner and Sandt, 1991).

Although early juvenile conch were normally buried during the day in the shallowest subtidal habitat and in sparse seagrass at Neighbor Cay, we have observed 12–25 mm conch on the surface in deeper seagrass beds with high shoot densities near Lee Stocking Island (Stoner, unpubl. data). Similar mention of epifaunal habits in early juveniles was made by Brownell (1977). It seems likely, therefore, that queen conch have different strategies of defense depending upon habitat. Conch recruiting to shallow sand habitats bury themselves in the substratum for protection from diurnal predators, and demonstrate strong, diurnal rhythms. Conversely, small conch inhabiting relatively dense seagrass beds find shelter among the seagrass blades. Burrowing would be inhibited by rhizome mats and anoxic sediments typical of seagrass beds with high biomass.

Although early juvenile conch appear to have considerable behavioral flexibility in avoiding predators, two lines of evidence suggest that early juveniles become less vulnerable to at least a certain suite of predators by the time they reach 50 or 60 mm SL. First, queen conch of approximately 60 mm have been the smallest individuals typically found on the surface during the day. Second, resistence to shell crushing is relatively low and constant up to 55 mm, then increases rapidly with conch size (Jory and Iversen, 1988). Thus, conch begin epifaunal existence once they are past the stage of highest vulnerability. As shown in our enclosure experiments, shallow sand bars probably become inadequate for juvenile conch by the time they reach 50 or 60 mm. Higher food intake, therefore, probably necessitates the move to vegetated habitats. However, as observed at Neighbor Cay, mortality can be very high during the ontogenetic habitat shift.

The proportion of early juvenile conch inhabiting sand bars and seagrass habitats is unknown. Our conclusions on the importance of the sand or seagrass interface, or both, to conch growth and survival is supported by two lines of circumstantial evidence. First, Stoner and Waite (1990) reported increasing length frequency of 1+ year class queen conch from sand bars to adjacent seagrass habitats. Data reported here show that the age-specific trend continues into the 0+ year class and supports the significance of ontogenetic shift. Second, large-scale distributional patterns in 1+ year class queen conch in the Exuma Cays show that nearly all major nurseries are located in seagrass meadows immediately adjacent to coarse-grained, shallow sand bars or beaches (Stoner et al., 1993). The compromise between protection offered by infaunal existence and food availability on the sediment surface appears to be an important mechanism regulating the distribution and abundance of juvenile queen conch in the vicinity of Lee Stocking Island.

Successful stock enhancement with *Strombus gigas* will depend upon releasing young-of-the-year juveniles into suitable habitats (Siddall, 1983). Hatchery production of juvenile conch is now relatively well refined (Davis et al., 1987; Davis 1993), but release procedures are not (Stoner, unpubl. data). Given the high vulnerability of conch less than 50–60 mm, extreme care must be taken to insure placement of small conch for stock enhancement in habitats with adequate food and shelter from predators. Sediment characteristics will be particularly important in the site selection because of the normal burrowing activity of early juvenile stages. Sediments should have high porosity and be well oxygenated. Additionally, releases would best be made at night when the conch are normally on the sediment surface. It is clear from this study that the behavior and habitat requirements of early juveniles are different from those of 1-year-old conch and provision must be made for ontogenetic habitat shifts. Sand bars close to seagrass meadows probably provide the optimal habitat for early juvenile conch in the Bahamas.

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Abstract.—Sectioned sagittae of 1,039 Spanish mackerel, *Scomberomorus maculatus* (Mitchill), from the Atlantic coast of the southeastern United States (North Carolina to Florida) were examined. The oldest male was age 6 and the oldest female age 11. Marginal increment analysis indicated that annulus formation peaks in May–June. The von Bertalanffy growth equation parameters (L_∞, k, and t_0, respectively) were: 538 mm fork length (FL), 0.31, and −2.31 for males; 723 mm FL, 0.24, and −1.80 for females; and, 760 mm FL, 0.18, and −2.44 for sexes combined. Gonads from 1,742 specimens were examined histologically to assess reproductive state. Mature gonads were present in 89% of age-0 males and 100% of older ages, whereas 5% of females were mature at age 0, 95% at age 1, and 100% at older ages. Females matured at 288–450 mm FL and males matured at 209–336 mm FL. Estimates of length at 50% maturity (L_{50}) were 35.8 cm FL for females and 23.9 cm FL for males. Females were in spawning condition from May to August; ripe males were captured April–November. Resting specimens were included in the assessment of maturity and the disadvantages of their inclusion are discussed.

Age, growth, maturity, and spawning of Spanish mackerel, *Scomberomorus maculatus* (Mitchill), from the Atlantic Coast of the southeastern United States*

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The Spanish mackerel, *Scomberomorus maculatus* (Mitchill), is a migratory scombrid of importance to commercial and recreational fisheries in the Gulf of Mexico and along the Atlantic coast of the southeastern United States (Trent and Anthony, 1978). Concerns about overfishing have prompted the establishment of size and bag limits, as well as recreational and commercial landings quotas, with regulations based on the hypothesis that there is an Atlantic migratory group and one or more Gulf of Mexico groups (SAFMC, 1988). Previous studies of the age and growth of Spanish mackerel have been based on specimens from the Gulf of Mexico, or from southeastern Florida where migratory groups are thought to overlap (Klima, 1959; Powell, 1975; Fable et al., 1987; Helser and Malvestuto, 1987). Whole sagittae were examined in these studies, but Collins et al. (1989) found that ages from sectioned otoliths were more accurate than those from whole otoliths for the congeneric king mackerel (*S. cavalla*). Thus, age and growth of Atlantic group Spanish mackerel have not been rigorously examined.

The annual reproductive cycle of Spanish mackerel has been described (Klima, 1959; Beaumariage, 1970; Powell, 1975; Finucane and Collins, 1986), but it has not been clearly established histologically for the Atlantic group. Klima (1959) and Powell (1975) collected specimens from southern Florida, an area where migratory groups may overlap. Of the four studies cited, only Powell (1975) used a histological technique. In previous studies of size and age at maturity, specimens were not clearly from the Atlantic group and age at maturity was not quantified (see Klima, 1959; Powell, 1975), and few small females were examined (see Klima, 1959; Finucane and Collins, 1986). The present study describes the age, growth, size and age at maturity, and reproductive cycle of Spanish mackerel from the Atlantic coast of the southeastern United States.

Methods

Specimens were collected with hook-and-line, trawls, gill nets, and block (stop) nets. Spanish mackerel abundance varies seasonally through most

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of their range owing to their migratory nature, so specimens were also acquired from recreational anglers, commercial gill netters, and seafood dealers throughout the southeastern United States. In addition, Spanish mackerel otoliths collected by the National Marine Fisheries Service (NMFS) Panama City (Florida) Laboratory were made available for this study. All specimens used in the present study were collected between Beaufort, North Carolina and Riviera Beach, Florida. All length measurements refer to fork length (FL). Except for those provided by NMFS, which were measured to the nearest cm, all fish were measured to the nearest mm.

One sagittal otolith from each fish was embedded in paraffin and sectioned (ca. 0.3 mm thick) with a Buehler Isomet saw equipped with a diamond blade. Sections were placed in cedar wood oil and examined under a dissecting microscope with both transmitted and reflected light. Most specimens provided by NMFS were processed similarly, but some consisted of otolith sections mounted on glass slides and were not immersed in cedar wood oil. Ages were assigned by two independent readers without reference to fish lengths or dates of capture. Otoliths considered aberrant by either reader or for which the readers disagreed on ages were deleted from the analyses. Distances from the focus to the margin (otolith radius) and to the distal edge of the opaque portion of each annulus were measured along the dorsal side of the sulcus acousticus with an ocular micrometer at 50× magnification.

Back-calculated lengths at age were computed for males, females, and sexes combined by the Fraser-Lee method (Poole, 1961; Carlander, 1982). The SYSTAT NONLIN module using the quasi-newton method (Wilkinson, 1987) was used to fit von Bertalanffy equations to individual back-calculated lengths at age.

For all specimens except those from NMFS (n=1,742), the posterior portion of the gonads was fixed in 10% seawater-formalin for 1–2 weeks and transferred to 50% isopropanol for 1–2 weeks; samples from NMFS (n=177) consisted only of otolith sections with associated length and macroscopically determined sex (male vs. female) data. Gonad samples were processed with an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Three transverse sections (6–8 µm thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with Harris hematoxylin, and counterstained with eosin-y.

Sex and reproductive state were assessed by one primary reader using histological criteria (Table 1). Sections from 50 randomly selected specimens were examined by a second reader early in the study to verify the assessments of the primary reader. Because only nine ripe female Spanish mackerel were captured, the occurrences of developing and spent females were also used to define the spawning period. Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the yolk vesicle stage and specimens with beta, gamma, or delta stages of atresia. The SYSTAT NONLIN module (Wilkinson, 1987) was used to fit a logistic model (% mature=100%/ $1 + e^{-g(L-L_{50})}$) to maturity data in 10 mm length intervals to estimate length at 50% maturity (L_{50}).

Because we were not able to obtain an adequate number of female specimens near the beginning of the spawning season to permit assessment of size/age at maturity, we used specimens collected throughout the year. To use all resting specimens in this assessment, we developed a criterion to distinguish the small percentage (<10%) of resting females with no atresia from immature (had never spawned) females. The criterion was based on the size of chromatin nucleolar (CN; as defined by Wallace and Selman 1981) oocytes, or oogo-

Table 1

Histological criteria used to determine reproductive state in Spanish mackerel, *Scomberomorus maculatus*. CN = chromatin nucleolar. References: Wallace and Selman (1981); Hunter and Macewicz (1985); Wenner et al (1986); West (1990).

Reproductive state	Female	Male
Immature	No atresia; predominance of CN oocytes and oogonia, most <70 µm.	Little or no spermatocyte development; empty lobules not present.
Developing	Primarily yolk vesicle and vitellogenic oocytes.	Spermatocyte development through lobules filled with spermatozoa.
Ripe	Mature oocytes (yolk droplets coalesce and peripheral migration of nucleus); hydrated oocytes.	Predominance of spermatozoa; little spermatogenesis.
Spent	Alpha atresia in >50% of vitellogenic and mature oocytes; beta atresia.	No spermatogenesis; residual spermatozoa in lobules and efferent duct.
Resting	Primarily CN (most >70 µm) and perinucleolar oocytes; beta, gamma, and delta atresia.	Some mitotic regeneration of spermatogonia and interstitial tissues; lobules and efferent duct empty.

nia if CN oocytes were not present. Perinucleolar oocytes were not included because this stage was not present in all immature females.

To develop the criterion, histological sections of ovaries from randomly-selected resting (n=21; 319–449 mm) and immature (n=32; 252–410 mm) females were examined and the area of one lobe was measured with an image analysis system. Five specimens were selected, if available, per 25-mm size interval for each of the two reproductive states. Atresia, which is evidence of previous oocyte development, was present in each resting female, but it was not present in each immature female. The oocytes and/or gonad area in resting females were noticeably larger than those in immature females; additionally, body length (<ca. 290 mm) indicated that some specimens were immature. For each specimen, a histological section and one of two axis orientations on the section were also randomly selected. The minimum and maximum dimensions of each of the five largest CN oocytes along the selected axis were measured and an average diameter was calculated for each oocyte. The largest CN oocytes were selected because previous studies have shown that the size of the largest oocyte can be used to assess ovarian development (see MacGregor, 1957; Greeley et al., 1987). We measured five oocytes instead of one oocyte to more accurately assess the size of the largest oocytes.

The accuracy of the criterion was assessed by comparing the length-frequency distributions of resting females and females with evidence of certain maturity (e.g., developing, ripe, or spent state). Because oocyte diameter and gonad area data were not normally distributed, the Mann-Whitney test was used in statistical analyses.

Results

Otoliths from 1,039 Spanish mackerel were examined, of which 132 were unreadable (i.e., considered aberrant by one or both readers). Readers agreed on ages for 96.5% of readable otoliths. Except for the small, secondary peak caused by the November sample of only seven individuals, the distribution of monthly percentages of otoliths with opaque margins was unimodal. Annual ring formation peaking in May–July is indicated (Fig. 1). Linear regressions of FL on otolith radius (OR) were male FL = 113.8 + 8.3 OR, n=228, r^2=0.55; female FL = 36.2 + 11.6 OR, n=502, r^2=0.71; combined FL = 40.1 + 11.2 OR, n=748, r^2=0.66. Females grew more rapidly and lived longer than males (Table 2). The oldest males were age 6 (n=3) and the oldest females, age 11 (n=2). The von Bertalanffy growth equation parameters (L_∞, k, and t_0, respectively)

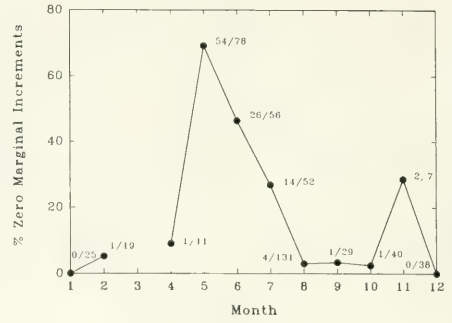

Figure 1

Monthly percentages of Spanish mackerel with marginal increments of zero (= opaque margins), with number of zero marginal increments over number in sample for each month.

were 538 mm, 0.31, and –2.31 for males; 723 mm, 0.24, and –1.80 for females; and, 760 mm, 0.18, and –2.44 for sexes combined. The von Bertalanffy estimates of L_∞ were reasonable compared with maximum observed lengths. One male (600 mm) and two females (760 and 730 mm) exceeded the asymptotic lengths.

All female specimens were used in the assessment of maturity because resting and immature females could be distinguished based on the size of the largest CN oocytes or oogonia if atresia was not present. The largest CN oocytes or oogonia in resting ovaries (with atresia) were significantly larger than those in immature ovaries (Fig. 2; U=633, P<0.001, df=1). The average diameter of these oocytes was usually >70 µm in resting ovaries. It was not necessary to use the CN oocyte/oogonium criterion often because >90% of the resting ovaries had beta or delta stage, and with less frequency gamma stage, atretic follicles. Gonad area was also larger in resting ovaries compared to immature ovaries (U=43, P<0.001, df=1; immature= 3.78+ 3.24 mm^2 per lobe; resting=9.93+3.33 mm^2 per lobe); however, oocyte characteristics should be used to assess reproductive state.

Use of the CN oocyte/oogonium criterion to assess maturity was not free of error, as the CN oocyte/oogonium size distributions for resting and immature females overlapped at 60–80 µm (Fig. 2). This error was negligible because the length-frequency distributions of resting females and females with evidence of certain maturity (e.g., developing, ripe, or spent state) overlapped, and the smallest individuals of both groups were in the same size interval (Fig. 3).

Female spanish mackerel become sexually mature later and at a larger size than males. Mature gonads

Table 2

Mean observed lengths at capture (mm FL) and mean back-calculated lengths at age for Spanish mackerel, by sex and for sexes combined.

Age	No. of specimens	Mean observed length at capture	Mean back-calculated lengths at successive annuli										
			1	2	3	4	5	6	7	8	9	10	11
Males													
1	58	372	332										
2	45	409	344	396									
3	37	430	345	393	423								
4	34	454	346	397	426	449							
5	22	504	364	416	448	475	499						
6	3	469	329	383	411	430	449	466					
	Total number		199	141	96	59	25	3					
	Weighted mean		343	399	429	458	493	466					
Females													
1	129	402	343										
2	124	465	362	444									
3	93	520	371	453	508								
4	49	560	366	446	501	546							
5	32	595	364	441	495	537	581						
6	7	636	363	448	500	548	594	630					
7	4	685	390	468	528	570	610	646	679				
8	3	690	328	419	482	529	569	609	642	675			
9	0	—	—	—	—	—	—	—	—	—	—		
10	0	—	—	—	—	—	—	—	—	—	—	—	
11	2	745	364	446	503	541	573	606	632	665	686	718	740
	Total number		443	314	190	97	48	16	9	5	2	2	2
	Weighted mean		359	447	503	544	584	627	657	671	686	718	740
Sexes combined													
1	190	393	337										
2	171	450	353	430									
3	134	494	358	433	482								
4	83	517	349	421	468	506							
5	54	558	354	424	472	510	548						
6	10	586	345	424	470	510	550	581					
7	4	685	392	469	529	571	610	646	679				
8	4	687	337	426	514	538	577	615	646	677			
9	0	—	—	—	—	—	—	—	—	—	—		
10	0	—	—	—	—	—	—	—	—	—	—	—	
11	2	745	366	441	504	542	574	606	632	665	686	718	740
	Total number		652	462	291	157	74	20	10	6	2	2	2
	Weighted mean		349	429	477	511	553	603	657	673	686	719	740

were present in 5% of the females at age 0, 95% at age 1, and 100% at age ≥2 (Table 3). Eighty-nine percent of the males were mature at age 0 and 100% at age ≥1 (Table 4). Estimates of L_{50} were 35.8 + 0.2 cm (SE) for females and 23.9 + 0.3 cm (SE) for males. The smallest mature female was 288 mm, and the largest immature female was 450 mm (Table 3). The smallest mature male was 209 mm, and the largest immature male was 336 mm (Table 4).

The combined percentage total of developing, ripe, and spent females by month indicated that May through August was the spawning period (Fig. 4). Ripe females were collected in inner continental shelf waters with a depth of ca. 9 m. They were collected in August in Onslow Bay (North Carolina) and off Cumberland Island (Georgia), and in May off Charleston (South Carolina). Males were present in ripe condition for a longer period (April–November) than were females (Fig. 4).

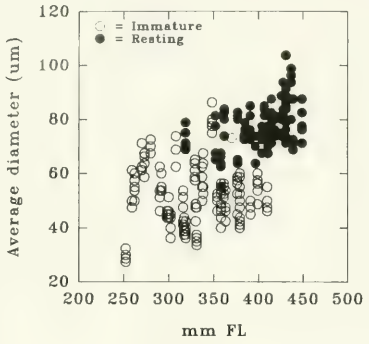

Figure 2

Individual average diameters (minimum + maximum dimensions/2) of the five largest chromatin nucleolar oocytes or oogonia along a randomly selected axis of a histological section from immature (n=32) and resting (n=21) Spanish mackerel, *Scomberomorus maculatus*.

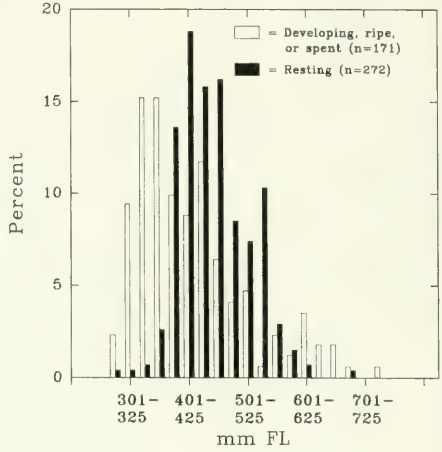

Figure 3

Length-frequency distributions for female Spanish mackerel, *Scomberomorus maculatus*, with evidence of certain maturity (e.g., developing, ripe, or spent state) and those in the resting state. All specimens examined histologically.

Table 3

Percentage of mature specimens by size class in 1136 female Spanish mackerel, *Scomberomorus maculatus*. Specimens in the developing, ripe, spent, or resting reproductive states were considered mature. All specimens were examined histologically. n = number of specimens.

mm FL	Age 0		Age 1		Age >1		No age	
	%	n	%	n	%	n	%	n
151–175							0	(2)
176–200							0	(10)
201–225							0	(72)
226–250							0	(117)
251–275	0	(1)					0	(125)
276–300	0	(16)	67	(3)			4	(84)
301–325	7	(55)	83	(6)			14	(56)
326–350	2	(48)	87	(15)			29	(56)
351–375	5	(20)	85	(13)	100	(1)	70	(33)
376–400	0	(11)	100	(19)	100	(16)	88	(25)
401–425	100	(1)	100	(26)	100	(21)	96	(24)
426–450	100	(1)	100	(20)	100	(28)	94	(18)
451–475			100	(15)	100	(30)	100	(12)
476–500			100	(5)	100	(23)	100	(7)
501–750			100	(1)	100	(68)	100	(32)
Totals	5	(153)	95	(123)	100	(187)		673

Table 4

Percentage of mature specimens by size class in 606 male Spanish mackerel, *Scomberomorus maculatus*. Specimens in the developing, ripe, spent, or resting reproductive states were considered mature. All specimens were examined histologically. n = number of specimens.

mm FL	Age 0		Age >0		No age	
	%	n	%	n	%	n
151–175					0	(1)
176–200					0	(12)
201–225					18	(50)
226–250					62	(68)
251–275	100	(1)			79	(93)
276–300	33	(3)	100	(1)	84	(57)
301–325	87	(23)	100	(3)	100	(21)
326–350	96	(23)	100	(13)	94	(18)
351–375	100	(2)	100	(18)	100	(23)
376–400			100	(28)	100	(27)
401–425			100	(35)	100	(9)
426–600			100	(54)	100	(23)
Totals	89	(52)	100	(152)		(402)

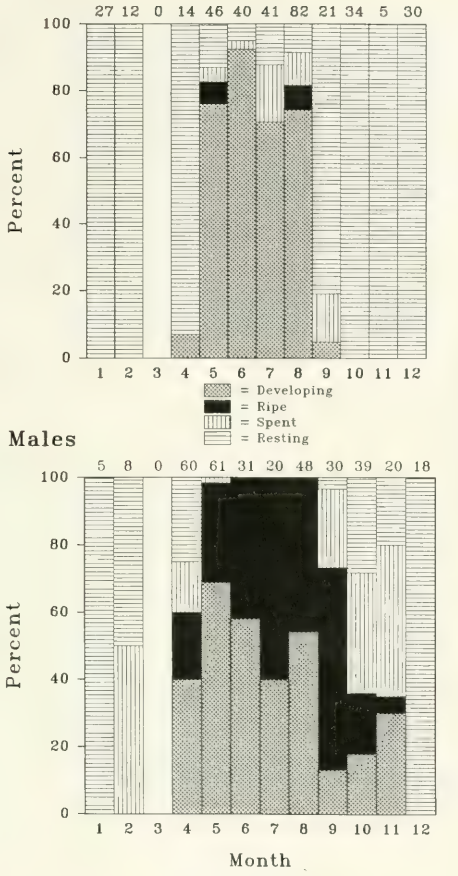

Figure 4

Percentage composition of reproductive states by month for 340 female and 352 male Spanish mackerel, *Scomberomorus maculatus*, based on histological criteria. Number of specimens examined is above the bar.

Discussion

While we lack direct evidence that growth rings on otoliths are deposited annually, indirect evidence supports that hypothesis. Otolith radius and FL are proportional as defined by the linear regression analysis, and the mean observed and back-calculated lengths at age agreed reasonably. In addition, the growth rings on otoliths apparently formed during a 2 to 3 month period. The relatively high (29%) percentage of otoliths with opaque margins in November was likely an artifact of the very small sample size (7) for that month.

The period of annulus formation that we observed agrees well with previous reports. Powell (1975) found that annuli formed during May–July in "Florida" (i.e. Gulf of Mexico and Atlantic) Spanish mackerel. Annulus formation may be slightly earlier (March–May) in fish from the northern Gulf of Mexico (Fable et al., 1987).

We found two 11-year-old fish, extending the reported longevity of Spanish mackerel slightly. Klima's (1959) oldest fish were 6 years old, Powell's (1975) was 8 years old, and Fable et al. (1987) reported one 9-year-old fish. Our mean back-calculated lengths at age tended to be slightly smaller than those of Powell (1975) after his standard lengths were converted to fork lengths (using his equations), and our values for von Bertalanffy asymptotic lengths (L_∞) were similar to his (555 mm for males, 694 mm for females). In comparison to the back-calculated lengths (Atlantic and Gulf of Mexico samples combined) of Fable et al. (1987), our back-calculated lengths were greater at age 1 and smaller at older ages. Their estimate of asymptotic length for females was similar to ours, but their estimate for males (794 mm) was much larger. Fable et al. (1987) reported greater asymptotic lengths for males than for females, while other studies found the reverse to be true (Powell, 1975; Helser and Malvestuto, 1987; present study). Powell (1975) excluded the oldest fish from all analyses owing to small sample sizes (19 fish age 6–8). Fable et al. (1987) used all age classes regardless of sample size and concluded that the resulting growth parameters were more realistic than those reported by Powell (1975). Whether the differences in growth parameter estimates between this and previous studies are due to methodological differences (e.g., sectioned vs. whole otoliths) or to differences in geographical coverage is not known.

Examination of 547 female Spanish mackerel <325 mm FL in the present study confirmed the lower limit of size at maturity reported by Finucane and Collins (1986), who based their estimate on nine specimens <325 mm FL from Georgia and the Carolinas (Table 5). Our estimate of size at maturity for females was higher than the estimate of Klima (1959). We found that males matured at smaller sizes than reported by Klima (1959) and Finucane and Collins (1986). These differences probably reflect the greater accuracy resulting from our histological versus their macroscopic methods.

Our age-at-maturity data generally concurred with the qualitative data in previous studies showing that female and male Spanish mackerel mature at ages 0–1 (Table 5). Using a histological method, Powell (1975)

Table 5
Summary of information available on size/age at maturity in Spanish mackerel, *Scomberomorus maculatus*.

Study and location	Size at maturity (mm FL)		Age at maturity (yr)	
	female	male	female	male
Present study; N. Carolina to SE Florida	288–450	209–336	0–1	0
Finucane and Collins (1986); Georgia and Carolinas	275–424	275–399	—	—
Powell (1975); South Florida, both coasts	—	—	1–?	—
Klima (1959); SE Florida	250–320	280–340	[1]1–2	[1]1–2

[1]Ages should be reduced by one year (see Powell [1975]).

found vitellogenic and/or mature oocytes in >50% of age-1 females sampled in Florida (Atlantic and Gulf coasts) during April through September. Klima (1959), using a macroscopic method, found that unreported percentages of ages 1–2 females and males were mature; however, Powell (1975) concluded that the ages in Klima (1959) should be reduced by one year. Thus, according to Powell (1975), the data reported by Klima (1959) showed that some age-0 specimens were mature. We found that more males than females (89% vs. 5%) were mature at age 0; most females matured at age 1.

Our data on the annual reproductive cycle agreed well with previous conclusions based on gonad condition (Beaumariage, 1970; Finucane and Collins, 1986) and on occurrence of larvae (Collins and Stender, 1987). Spawning occurs in Atlantic group females from mid-spring through summer. For males, we concurred with Finucane and Collins (1986) that developing or running ripe males are present from mid-spring through early fall.

Our method of assessing maturity was less efficient and perhaps less accurate than the method used by Hunter et al. (1992) for Dover sole, *Microstomus pacificus*. Hunter et al. (1992) collected specimens prior to the spawning period, when oocyte development was at the vitellogenic stage. Ovaries without yolked oocytes, postovulatory follicles, or atresia were considered immature. The primary advantages of their method are that specimens are collected over a shorter period of time and that it is not necessary to develop a criterion to distinguish resting and immature females. We were unable to acquire a sufficient number of specimens at the appropriate time to use their methodology.

Our conclusions concerning size and age at maturity were based on samples solely from the Atlantic migratory group, on ages from sectioned sagittae, and on histological examination of gonad tissue. Most female Spanish mackerel mature at age 1 and at lengths greater than 36cm FL (L_{50}). The minumum legal length for Spanish mackerel is currently set at 12 inches (30.5 cm) FL by the South Atlantic Fishery Management Council and most southeastern Atlantic states have adopted the same regulation. Thus, the harvest of age-0 immature females is permitted. Federal and state agencies responsible for the management of Atlantic group Spanish mackerel may wish to re-examine minimum length regulations in light of our results.

Acknowledgments

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A comparison of alternative methods for the estimation of age from length data for Atlantic coast bluefish (*Pomatomus saltatrix*)

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Abstract.—Bluefish (*Pomatomus saltatrix*) are found along the US Atlantic coast from Maine to Florida, and are the object of a major recreational fishery as they migrate northward from the South Atlantic Bight in the spring and return southward in the late fall. Acceptance of analytic assessment results for bluefish has been hindered by the lack of a consistent time series of geographically comprehensive age-length keys for converting bluefish lengths to age. We used bluefish length-age data from North Carolina commercial fisheries during 1986 to 1989 to compare the utility of two simple methods for estimating age from length-frequency data with two more rigorous statistical methods. The simple methods were cohort slicing using von Bertalanffy growth parameters for bluefish and the application of a pooled age-length key compiled with data from different times and fishing areas. The two statistical approaches were the iterated age-length key method and MULTIFAN. Combined 1986–1989 proportions at age estimated by cohort slicing, pooled age-length key, and iterated age-length key methods were significantly different from those in the test data, based on a quantitative comparison using the Kolmogorov-Smirnov cumulative distribution test. Proportions at age estimated by MULTIFAN were not significantly different from the test data. Our work suggests that MULTIFAN is the best alternative to a time series of fishery-specific age-length keys for the estimation of Atlantic coast bluefish ages from length data.

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Fishery Bulletin 91:534–549 (1993).

Bluefish (*Pomatomus saltatrix*) are found along the U.S. Atlantic coast from Maine to Florida, migrating northward from the South Atlantic Bight in the spring and returning southward in the late fall. They are the target of a major recreational fishery along the Atlantic coast, with catches averaging 47,000 metric tons (t) per year during 1980 to 1990. For the same period, the commercial catch of bluefish, mainly by otter trawls, averaged 6,400 t per year.

Atlantic coast bluefish exhibit fast growth during the first two years of life, attaining fork lengths of over 40 cm by age 2 (Hamer, 1959; Lassiter, 1962; Richards, 1976; Wilk, 1977). They may reach ages of up to 12 years and sizes in excess of 100 cm fork length and 14 kg in weight. About fifty percent of bluefish reach sexual maturity by the second year of life (Wilk, 1977). Spawning occurs during two major periods: March and April in the South Atlantic Bight near the inner edge of the Gulf Stream, with a peak about 1 April; and June through September in the Mid-Atlantic Bight, with a peak about 1 August (Wilk, 1977; Kendall and Walford, 1979; Nyman and Conover, 1988). There is evidence that spring and summer spawning fish mix extensively during their lifespan, as summer spawning fish have been observed to originate from both cohorts (Chiarella and Conover, 1990). Year classes of bluefish therefore consist of varying proportions of spring- and summer-spawned cohorts.

In anticipation of a fisheries management plan to regulate commercial and recreational catches of Atlantic coast bluefish, the Atlantic States Marine Fisheries Commission (ASMFC) and the Mid-Atlantic Fisheries Management Council (MAFMC), in cooperation with the National Marine Fisheries Service (NMFS), began work on stock assessment in 1986. Length-frequency data collected by the Northeast Fisheries Science Center (NEFSC) (bottom trawls, 1976–1986) and by NMFS Marine Recreational Fishery Statistics Survey (MRFSS) (1979–1985) were available for analytical assessment (i.e., virtual population analysis). However, no consistent time series of geographically comprehensive age-length keys were available for estimating age-frequency from length-frequency data. Therefore, an age-length key (hereafter referred to as the ASMFC pooled key) was devel-

oped by pooling data collected by the fisheries agencies of several Atlantic coast states during 1982 to 1986 (Crecco et al.[1]; Terceiro[2]).

There were concerns about the potential for biased results in using the ASMFC pooled key, because of the influence of interannual variation in growth, recruitment, or mortality rate, given the broad temporal and geographic scale over which the age-length data were collected (Westrheim and Ricker, 1978). As a result, no consensus was reached on the utility of the ASMFC pooled key, catch-at-age data, or subsequent analyses presented in Crecco et al.[1] and Terceiro[2].

Following implementation of the bluefish Fisheries Management Plan in 1990, stock assessment work for bluefish was renewed by ASMFC. A yield-per-recruit analysis was developed to provide biological reference points for the new assessment. Parameters of the von Bertalanffy growth function $L_t = L_{inf}[1-e^{-K(t-t_0)}]$, derived from weighted mean calculated lengths at annulus formation presented in NOAA (1989), were used as an expedient alternative to the ASMFC pooled key to age MRFSS-sample bluefish length-frequency data by cohort slicing (i.e., solving for t in the von Bertalanffy growth equation, given L_{inf}, L_t, K, and t_0). Length at age, weight at age, and partial recruitment vectors for the yield-per-recruit analysis were developed from this version of the MRFSS length-age data.

Published estimates of mean calculated bluefish length at annulus formation exhibit considerable variation (Barger, 1990; Chiarella and Conover, 1990; Hamer, 1959; Lassiter, 1962; NOAA, 1989; Richards, 1976; Wilk, 1977) (Table 1). The variation is likely due to 1) variation in growth over time, 2) sampling and availability bias, 3) varying influence of Lee's phenomenon (Jones, 1958), 4) use of different conventions in fixing the assumed birthdate of bluefish, and 5) differential proportions of spring and spawned fish in the length frequency samples collected by different investigators (Wilk, 1977; Kendall and Walford, 1979; Chiarella and Conover, 1990). Variation in mean lengths at age and subsequently derived growth parameters, likely inherent when data from several disparate sources are considered, could lead to biased results from cohort slicing. The Eleventh NEFSC SAW[3] recommended testing alternative methods, such as mixture of distributions methods, and data sources in lieu of a time series of age-length keys for the estimation of bluefish ages from length-frequency data.

This work compares results from the application of 1) the cohort slicing method using growth parameters, 2) a pooled age-length key applied in the standard manner, 3) the iterated age-length key method (IALK) as presented by Kimura and Chikuni (1987) and Hoenig and Heisey (1987), and 4) MULTIFAN, a mixture of distributions method (Fournier et al., 1990), to bluefish length-age data collected by the North Carolina Division of Marine Fisheries (NCDMF) from 1986 to 1989. Our objective was to determine how these methods interpret the known-age test data, and suggest whether any are an acceptable alternative to the resource-intensive method of developing fisheries specific age-length keys.

Methods

Data sources

North Carolina bluefish length-age test data Bluefish are landed in the commercial long haul seine (April–October), pound net (May–October), and winter otter trawl (October–May) fisheries in the estuarine and coastal waters of North Carolina. The NCDMF has collected biological sample data from these commercial fisheries for bluefish since 1982. This time series is the largest and most consistent body of bluefish length-age data available. NCDMF bluefish length-age data collected from spring 1986 to winter 1989 (n = 1469, 13–84 cm, ages 0 to 9, ages determined from scale annuli), aggregated by calendar year, were used as a test data set for comparing the performance of alternative methods for estimating bluefish ages from length data (Table 2, Figure 1).

Investigators have not agreed on a birthdate convention for Atlantic coast bluefish. NCDMF fisheries biologists employ an unweighted average date of 1 June, between peak spawning of the spring (1 April) and summer (1 August) aggregations. This date roughly corresponds with the time of annulus formation during late May to mid-June.

Bluefish recruit to North Carolina fisheries during the summer fishing season. Bluefish with fork lengths ranging from 15 to 32 cm that are captured before 1 June and possess scales that do not yet exhibit the first annulus are typically classified as age 0. Inspection of modes in length-frequency data and the timing of spawning suggests that the largest of these bluefish originate from the spring cohort of the previous calendar year, while the smallest are fish from the summer

[1]Crecco, V., M. Terceiro, and C. Moore. 1987. A stock assessment of Atlantic coast bluefish, *Pomatomus saltatrix*. Special report prepared for the Atlantic States Marine Fisheries Commission, Washington, D.C.

[2]Terceiro, M. 1987. Status of Atlantic coast bluefish—1987. U.S. Dep. Commer. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Cent., Woods Hole lab. Ref. Doc. 87-10, 54 p.

[3]NEFSC. 1990. Report of the Eleventh NEFSC Stock Assessment Workshop, Fall 1990; Woods Hole, MA. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 90-09, 121 p.

Table 1

Weighted mean calculated fork lengths (cm) at annulus formation of bluefish (*Pomatomus saltatrix*) from various studies for fish from the U.S. Atlantic coast.

		Age (yr)											
Source	*N*	1	2	3	4	5	6	7	8	9	10	11	12
Hamer 1959	?	31.8	38.1	41.9	50.6	55.0	63.2	70.0		72.6			
Lassiter 1962 spring spawned	290	26.6	37.6	48.4	53.5	61.2	68.2	74.1	79.2				
summer spawned	154	14.8	30.3	41.9	48.4								
Richards 1976	64	23.0	40.0	49.0	58.0	64.0	69.0	71.0					
Wilk 1977	7,425	20.8	33.6	44.4	55.1	63.1	67.3	71.9					
NOAA 1989	429	22.6	38.1	50.2	59.8	67.3	73.1	77.8	81.4	84.2	86.5		
Barger 1990	588	29.0	36.1	41.5	47.3								
Chiarella and Conover 1990	147	26.5	43.5	53.2	60.7	65.9	69.3	72.0	75.4	79.3	83.8	85.8	87.0

Table 2

North Carolina Division of Marine Fisheries 1986–1989 bluefish (*Pomatomus saltatrix*) length-age test data, n=1469.

	Numbers at age									
Length (cm)	0	1	2	3	4	5	6	7	8	9
14	1									
15	2									
16	11									
17	4	6								
18	15	5								
19	18	9								
20	10	8								
21	9	11								
22	11	5	1							
23	10	6								
24	18	6								
25	28	10								
26	38	14								
27	39	21								
28	54	10	1							
29	29	21	1							
30	21	21	1							
31	13	17	1							
32	17	28	2							
33	4	37	4							
34	3	32	3							
35	1	52	3							
36		43	4							

Table 2 (Continued)

	Numbers at age									
Length (cm)	0	1	2	3	4	5	6	7	8	9
37	1	35	2							
38		36	8							
39		45	1							
40		29	7							
41		24	8							
42		13	9							
43		8	3							
44		1	8							
45		6	4							
46		4	6							
47		1	7							
48		2	12							
49		1	7							
50			10							
51			11							
52			5							
53			2	2						
54			5	2						
55			2	3						
56				5						
57			2	9						
58			1	5						
59			1	6	1					
60				7	3	1				
61				2	5	1				
62			2	7	11					
63				5	9	2				
64				2	5	1				
65				3	12	4				
66				1	11	11				
67				1	9	16	2			
68					5	9	2			
69					6	11	10			
70					3	21	8			
71						16	14	1		
72						10	13	4		1
73						5	8	6		
74							6	8	1	
75						1	7	6	1	
76							3	5	3	
77						1	2	4	2	
78							3	3		1
79							1	1	2	3
80								1	4	1
81							1	1	2	
82									5	1
83									1	1
84								1		1
Age totals	357	567	144	60	80	110	80	41	21	9
Mean length (cm)	25.7	33.7	44.7	59.4	64.8	68.9	72.2	75.2	79.2	79.6
SD	3.6	6.5	3.7	1.1	1.0	1.2	1.1	0.7	0.5	0.4
CV (%)	14.0	19.3	8.3	1.9	1.5	1.7	1.5	0.9	0.6	0.5

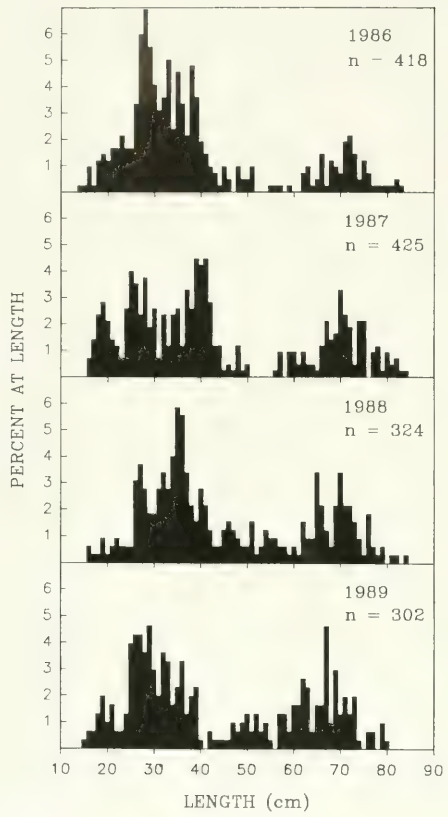

Figure 1
North Carolina Division of Marine Fisheries (NCDMF) 1986–1989 bluefish (*Pomatomus saltatrix*) length-age test data: percent at length distributions by year.

cohort of the previous calendar year. Depending on the exact time of spawning and sampling, the largest age-0 fish may be 12–15 months old, while the smaller age-0 fish are about 10 months old. Under the birthdate convention of 1 January used by NEFSC fisheries biologists, all of these fish would be classified as age class 1. This difference in classification schemes has caused confusion in previous stock assessments and other research for bluefish. The NCDMF length-age test data in this paper are based on the 1 June birthdate convention.

Connecticut, New Hampshire, North Carolina (CNN) length-age data Length-age sample data (n = 3883, 12–87 cm, ages 0 to 11, ages determined from scale annuli) were available for bluefish collected by state agencies in Connecticut (1984–1985, n = 1452), New Hampshire (1986, n = 76), and North Carolina (1982–1985, n = 2355) (Fig. 2). The 1 June birthdate convention was employed in aging. Connecticut and New Hampshire fish were collected in research surveys, mainly during the summer and fall when most recreational fishing occurs (June–October). North Carolina fish were taken throughout the year in proportion to the number of fish landed by commercial fisheries. These data were combined to form a matrix of the distribution of age at length for bluefish. This matrix was applied as a standard age-length key (CNN ALK) to the NCMDF 1986–1989 annual length distributions

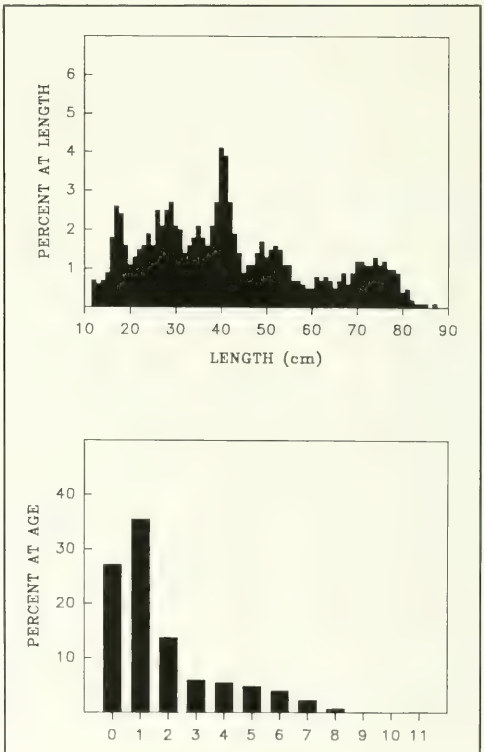

Figure 2
Connecticut, New Hampshire, and North Carolina length-age data (n=3,883) for bluefish (*Pomotomus saltatrix*) used as the basis for the Connecticut, New Hampshire, and North Carolina age-length key (CNN ALK) and the interated age-length key (IALK) method.

to estimate proportions at age for comparison with the NCDMF ages. It is important to note that the North Carolina part of the CNN length-age data and the NCDMF 1986–1989 length-age data were compiled by the same age-reader and therefore were not completely independent.

NOAA (1989) length-age data Bluefish length-age data collected during NEFSC autumn bottom trawl research surveys, 1985–1987, formed the basis for weighted, mean-calculated lengths at annulus formation presented in NOAA (1989). Samples were aged according to the 1 January birthdate convention. These data provided the von Bertalanffy growth parameters of L_{inf} = 94.6 cm, K = 0.242, and t_0 = –0.128, which were used in cohort slicing for estimation of bluefish ages from length data in the revised yield-per-recruit analysis for bluefish[3].

The NOAA (1989) value of t_0 was adjusted to reflect the difference between the 1 January (used by NEFSC) and 1 June (used by NCDMF) birthdate conventions. The difference of 151 days, or 0.414 years, was added to the ages of fish in the raw data used to estimate the parameters. Refitting the data provided a new value of t_0 = –0.542 (e.g., a 25-cm bluefish sampled on 1 April would typically be classified as age 0 by NCDMF staff; a 25-cm bluefish aged by cohort slicing with NOAA 1989 parameters and t_0 = –0.128 would be 1.140 years old, and classified as age 1; while a 25-cm bluefish aged by cohort slicing with NOAA 1989 parameters and t_0 = –0.542 would be 0.726 years old and classified as age 0). The NOAA 1989 growth parameters with the adjusted value of t_0 were used in cohort slicing of the NCDMF 1986–1989 annual length-frequency data for comparison with the NCDMF 1986–1989 annual and combined age distributions.

Statistical methods

Iterated age-length key The iterated age-length key (IALK) method was introduced by Kimura and Chikuni (1987). The method combines the standard age-length key (Kimura, 1977; Westrheim and Ricker, 1978) and mixture of distributions approaches (Hasselblad, 1966; Macdonald and Pitcher, 1979; Schnute and Fournier, 1980) for the resolution of lengths to ages. Application of the standard age-length key method without bias requires that the length-age data and length data have the same underlying age composition (Kimura, 1977). The IALK method has been presented as a potential solution to the problem of applying age-length keys to length-frequency distributions with different time and space characteristics, and therefore potentially different underlying age distributions (Kimura and Chikuni, 1987; Hoenig and Heisey, 1987).

Assumptions for the IALK method are somewhat less stringent than for standard application of the age-length key. The method requires only that the length-age data be adequately sampled and that the associated probabilities of length at age are applicable to the observed length distribution to be aged, although the potential for bias increases if the two data sets have very different temporal and geographic characteristics. The goal of the iterative procedure is to modify the length distribution of the length-age data so that it more closely approximates the length-frequency data to be aged, until the underlying age distributions of the length-age data and length-frequency data also become similar, thus satisfying the assumptions of the standard age-length key concept.

Kimura and Chikuni (1987) presented the IALK method in the form of an algorithm, gave conditions for which the algorithm converged to a unique solution, and showed the algorithm was an application of the expectation-maximization (EM) algorithm (Dempster et al., 1977) to mixtures of distributions. Hoenig and Heisey (1987) subsequently used a similar approach for the IALK as an EM algorithm, while making different assumptions about the sampling errors of the data. The steps of the IALK algorithm as implemented by Kimura and Chikuni (1987) are the following:

1) estimate the proportions at age, with all ages initially having equal probability. Hoenig and Heisey (1987) suggested that the initial estimate of proportions at age might be set the same as those in the length-age data;

2) using observed probabilities of length at age calculated from the length-age sample data and the current estimate of proportions at age, calculate the corresponding age-length key (probabilities of age at length). An intermediate result of this step is the IALK estimate of the observed length distribution;

3) apply the observed length distribution to be aged to the calculated age-length key of step 2;

4) calculate the maximum absolute deviation over ages between the newly estimated proportions at age of the observed length frequency and the proportions at age in the previous iteration. If the deviation is less than some small constant, then stop; otherwise continue with the next iteration of the age-length key.

We used the CNN length-age data (Fig. 2) as the source for the probabilities of length at age used in the calculation of the IALK applied to the observed NCDMF 1986–1989 length distributions (Fig. 1). Initial proportions at age were set to the same values as the CNN length-age data, as suggested by Hoenig and Heisey (1987), for ages 0 to 11:

[0.272 0.355 0.138 0.060 0.055 0.048 0.040
0.023 0.007 0.001 0.0001 0.0009].

The IALK algorithm was judged to have converged when the maximum absolute deviation summed over iterated proportions at age was less than 0.001 (0.1%). The IALK method was applied to the annual NCDMF 1986–1989 length distributions separately.

MULTIFAN MULTIFAN was introduced by Fournier et al. (1990) as an extension of the methods of Schnute and Fournier (1980) and Fournier and Breen (1983). MULTIFAN is a likelihood-based method using the mixture of distributions approach for the classification of lengths to age, with consideration of biological constraints, to simultaneously analyze several length-frequency distributions sampled at different times. The major assumptions of the method include the following: 1) the lengths of the animals in each age class are normally distributed about the mean length at age; 2) growth follows the von Bertalanffy function; and 3) standard deviation of lengths about the mean length at age varies as a simple function of mean length at age.

The log-likelihood function used in MULTIFAN compares the expected probability that a fish chosen randomly will lie in a given length interval with the observed number of fish in that interval for the set of growth parameters being tested. The formal statistical basis of MULTIFAN allows for a structured and relatively objective means of evaluating alternative interpretations of the processes producing the observed length- frequency distributions (e.g., the growth rate and resulting number of significant age classes, gear selectivity on younger age classes, and evidence of a length dependent trend in the standard deviation of length at age). The basic set of parameters of the MULTIFAN model include the following: 1) the proportions at age; 2) the mean length of the first age group; 3) the mean length of the last age group; 4) the von Bertalanffy growth parameter K; 5) two parameters which determine the standard deviation of length at age; 6) a parameter determining the extent of selectivity bias on the first age group; and 7) a parameter determining the overall variance of the sampling errors in the length-frequency data sets (see Fournier et al. 1990 for detailed notation of the MULTIFAN model parameterization).

For example, in the case of two suspected age classes underlying a set of five length-frequency distributions, the model would have a total of nine parameters. The addition of one age class to the model (one age, five distributions) would increase the number of parameters by five, to 14. Accounting for a length dependent trend in standard deviation of length at age (LDSD) in the three age-class case would increase the number of parameters by one, to 15; accounting for selectivity bias on the first age group would again increase the number of parameters estimated by one, to 16. A chi-square test is used to determine the best fitting growth structure. The statistical significance of increases in the log-likelihood values obtained by the addition of age classes are determined by the 0.90 point of the chi-square random variable, to reduce the probability of rejecting an additional age class when it is actually present in the data. The significance of the addition of other parameters is determined at the more conventional 0.95 level (Fournier et al., 1990).

After an initial inspection of modes apparent in the length-frequency data, initial constraints for MULTIFAN included reasonable ranges for 1) the number of expected age classes, 2) the corresponding values for the von Bertalanffy parameter K, and 3) a range for the mean length at age of an obvious mode. Initial constraints for the NCDMF 1986–1989 bluefish length-frequency data were potential significant age classes from 5 to 12, K range from 0.20 to 0.40, and mean length range for presumed age-0 fish in the 1986, 1987, and 1989 samples set at 15–30 cm, and for age 1 in 1988 at 30–40 cm. Preliminary MULTIFAN runs determined the number of significant age classes underlying the NCDMF 1986–1989 sample length frequencies. Additional runs with MULTIFAN were made to test for evidence of selectivity bias (SEL) on the first age class and for a length dependent trend in standard deviation of length at age (LDSD) as means of improving the fits.

Comparison of methods

A qualitative assessment of the utility of each method was made by inspection of the estimated mean lengths at age determined by the different alternatives. The result of ultimate interest from the application of these methods to the NCDMF length frequency distributions, however, is the number of fish per age class. We assessed the performance of the alternatives by using the Kolmogorov-Smirnov (K–S) cumulative distribution test (Sokal and Rohlf, 1981) to compare the calculated annual and combined 1986–1989 proportions at age from each aging approach with the NCDMF annual and combined 1986–1989 proportions at age.

This non-parametric method tests for differences in both the shape and location of two frequency distributions under the null hypothesis that the samples are taken from populations with the same underlying distribution. The proportions at age being compared are considered as two samples from the commercial landings. If the maximum unsigned difference between cumulative frequency distributions (proportions at age) exceeds some critical value (D) for a given confidence level and sample size, then the null hypothesis is rejected (Sokal and Rohlf, 1981). The test provides an

indication of how closely the alternative methods can match the interpretation of the age structure commercial landings of bluefish in North Carolina that would be provided by the NCDMF 1986–1989 length-age test data. By extension, the utility of these methods as alternatives to a time series of geographically appropriate age-length keys can be evaluated on a quantitative scale.

Results

Application of the alternative methods to the NCDMF 1986–1989 length data provided estimates of mean length at age that were lower than the NCDMF value for age-0 fish, and generally higher for ages 1 and older. Mean lengths at age estimated by MULTIFAN for ages 3 to 5 were the exception, as they were lower than the NCDMF values (Table 3).

For the annual and combined NCDMF 1986–1989 length distributions, cohort slicing using the NOAA (1989) growth parameters consistently provided the poorest match with the NCDMF proportions at age (Tables 4–8, pages 543–547); there were large differences relative to the NCMDF data for ages 0, 4, and 5. Differences were significant ($P > 0.05$) in 1988 and for the combined distribution.

Standard application of the CNN ALK provided improved results over simple cohort slicing, and estimated age proportions were not significantly different from the true NCDMF proportions, except when data were combined. Estimated proportions at age for fish of less than 40 cm were very close to the NCDMF proportions. The largest value of D always occurred at age 4 or 5, reflecting problems in resolving fish in the 60–75 cm length interval to the correct age when using the standard age-length key application of the CNN length-age data (Tables 4–8).

The IALK method provided initial results that were surprisingly poor. The convergence criteria proposed by Kimura and Chikuni (1987) for IALK estimated proportions at age were intended to stop iteration of the key when the underlying age distributions of the length-age data and the length frequency to be aged closely matched, thus better satisfying the conditions necessary for unbiased application of the key.

Two characteristics of bluefish biology, multiple spawned cohorts for the same year class and differential availability to fisheries by age class, appear to have combined to result in enough difference in the length distribution patterns of the CNN and NCDMF data to significantly hinder the effectiveness of the IALK model when the final iteration of the key was used. Iteration of the annual CNN length-age distributions reduced the number of bluefish in the 50–60 cm interval, and increased the number of bluefish in the 20–40 cm (ages 0 and 1) and 65–75 cm (ages 4 and 5) length intervals. The resulting length and age distributions of the input CNN length-age data matched the NCDMF lengths more closely than the initial distributions. However, when the final iterated key was applied to NCDMF lengths, the cumulative proportions at age generally provided large values of D for ages 0 and 1, or ages 4 and 5 (Table 9, page 548).

Intermediate iterations of the CNN length-age data (generally the first or second iteration) provided a better match to the NCDMF proportions at age than the final iteration (generally about the 15th iteration). In effect, we limited the degree to which the CNN length-age distribution could be changed by evaluating the application of each iteration of the CNN ALK, and selecting as the best solution the estimated proportions at age providing the smallest cumulative difference from the NCDMF cumulative proportions. Under this procedure of evaluation, the IALK provided the same or slightly improved results relative to standard application of the CNN length-age data. Only for the combined 1986–1989 length distributions were the IALK estimated proportions at age significantly different from the NCDMF proportions at the 5% level (Tables 4–8).

MULTIFAN results were inconsistent when considered on an annual basis. The growth parameters selected by MULTIFAN as best describing the growth pattern of bluefish during 1986–1989 (Table 10, page 549) performed relatively poorly in matching the NCDMF 1986 and 1987 proportions at age, but provided a close match to the NCDMF 1988 and 1989 proportions (Tables 4–8). Variation in growth and recruitment to the sampled fishery among cohorts contributed to varying success in matching the annual NCDMF proportions with the MULTIFAN method.

The best fitting MULTIFAN run provided the only non-significant value of D (at age 6, the "plus group" of the MULTIFAN model interpretation) for the combined 1986–1989 length distributions obtained among the compared methods. The largest values of D provided by the other methods occurred at ages 4 or 5, indicating problems in resolving the ages of fish 60 cm and larger in accordance with the NCDMF interpretation. Only MULTIFAN provided proportions at ages 4 and 5 that accurately reflected the NCMDF proportions in the combined distributions (Table 8). The improved performance of MULTIFAN when the NCDMF data are evaluated in combined fashion reflects better adherence to the underlying concept of the MULTIFAN model (Fournier and Breen, 1983).

Table 3

Combined mean fork lengths (cm) at age from application of alternative methods for conversion of North Carolina Division of Marine Fisheries (NCDMF) 1986–1989 bluefish (*Pomatomus saltatrix*) length-frequency data to ages, compared with NCDMF values.

	Mean fork length at age (cm)											
Method	0	1	2	3	4	5	6	7	8	9	10	11
CNN ALK	25.0	34.6	47.9	60.7	67.3	71.3	74.9	77.8	81.1	82.2	—	—
NOAA 1989 $t_0 = -0.542$	24.6	35.9	48.6	59.4	66.5	72.1	77.4	81.1	83.6	—	—	—
IALK	25.1	34.7	47.8	60.7	67.3	71.3	74.9	77.7	80.2	82.4	83.1	82.0
MULTIFAN	24.9	34.5	45.5	54.5	62.0	68.2	73.3	—	—	—	—	—
NCDMF 1986–1989	25.7	33.7	44.7	59.4	64.8	68.9	72.2	75.2	79.2	79.6	—	—

Discussion

Cohort slicing, standard application of the CNN ALK, the IALK method, and MULTIFAN are increasingly complex solutions to the problem of estimating ages from length data when appropriate age-length keys are not available. All four methods provided reasonable interpretations of the NCDMF bluefish data by accurately reflecting the dominance of age-0 and age-1 fish in the length distributions. Cohort slicing using the NOAA (1989) parameters generally provided the poorest match with the NCDMF proportions at age, because the method fails to account for the variability in length at age owing to multiple spawning events and the variation in growth among cohorts.

The CNN ALK and IALK provided satisfactory resolution of bluefish lengths to age, nearly matching those estimated by the best MULTIFAN fit for the combined NCDMF 1986–1989 data. Performance of the CNN ALK and IALK was poorest for those bluefish ages with a high degree of overlap in the NCDMF length distributions (usually ages 4 and 5) because of the inability of these methods to accurately portray the variation in growth among cohorts. However, the CNN ALK and IALK provided the most accurate estimates of mean length at age for very large bluefish (age 7 and older) which often may not be sufficiently abundant in length-frequency sample distributions to form significant modes.

We note that with the IALK method, the length-age data would usually be applied to a length distribution of unknown age composition, in which case the alternative method we used for selecting the best IALK solution would not be an option. Kimura and Chikuni (1987) suggested the IALK method should reduce bias in the resulting age distribution if an age-length key is applied to length-frequency data with potentially different underlying growth or selectivity patterns. Our work confirmed that the IALK algorithm achieves the goal of reducing the differences in underlying age distribution of the length-age data used as a key and the length frequency to be aged. However, when these differences are so large that even the less restrictive assumptions of the IALK method are violated, the IALK method provides little improvement over standard application of the age-length key.

MULTIFAN performed well in resolving the underlying age structure of bluefish length frequency samples, given the reasonable number (e.g., through age 5 or 6) of age groups that were apparent in the NCDMF 1986–1989 length samples. MULTIFAN was the only method to correctly estimate the relative proportions at ages 4 and 5, by accurately reflecting the variation in length at age of fish from the length frequency mode at 65–75 cm.

Key attributes of the MULTIFAN model which contributed to good performance in this exercise with bluefish data include 1) the large number of parameters estimated by the model, and consideration of variation of mean length at age and selectivity bias on the first age class, 2) use of the entire NCDMF length data series to estimate the growth pattern, and 3) the hypothesis testing approach to model evaluation. Based on qualitative evaluation of the estimates of mean lengths at age and the quantitative comparison of estimated proportions at age with the Kolmogorov-Smirnov cumulative distribution test, we believe that MULTIFAN was the best current alternative to a time series of fishery-specific age-length keys for the estimation of bluefish ages from lengths data.

The MULTIFAN model is a good starting point for future method development. MULTIFAN assumes

Table 4

North Carolina Division of Marine Fisheries (NCDMF) 1986 bluefish (*Pomatomus saltatrix*) proportions at age (*P*) and cumulative proportions at age (*C*) compared with estimates derived by cohort slicing using NOAA (1989) parameters, by standard application of the Connecticut/New Hampshire/North Carolina age-length key (CNN ALK), the CNN age-length key applied using the iterated age-length key method (IALK), and by MULTIFAN. Maximum difference in cumulative proportions at age (*D*) in underlined bold print. $D_{0.05,\,n\,48}$=0.094.

Age	NCDMF *P*	NCDMF *C*	NOAA 1989 *P*	NOAA 1989 *C*	NOAA 1989 *D*	CNN ALK *P*	CNN ALK *C*	CNN ALK *D*	IALK *P*	IALK *C*	IALK *D*	MULTIFAN *P*	MULTIFAN *C*	MULTIFAN *D*
0	0.323	0.323	0.361	0.361	**0.038**	0.313	0.313	0.010	0.318	0.318	0.005	0.258	0.258	**0.065**
1	0.428	0.751	0.416	0.778	0.026	0.459	0.773	0.022	0.455	0.773	0.022	0.490	0.749	0.002
2	0.072	0.823	0.045	0.823	0.000	0.053	0.825	0.002	0.053	0.825	0.002	0.065	0.813	0.010
3	0.012	0.835	0.017	0.840	0.005	0.026	0.852	0.017	0.026	0.852	0.017	0.007	0.821	0.014
4	0.036	0.871	0.055	0.895	0.024	0.053	0.904	**0.033**	0.053	0.904	**0.033**	0.005	0.825	0.045
5	0.065	0.935	0.079	0.974	0.038	0.053	0.957	0.022	0.053	0.957	0.022	0.067	0.892	0.043
6	0.038	0.974	0.014	0.988	0.014	0.024	0.981	0.007	0.024	0.981	0.007	0.108	1.000	0.026
7	0.007	0.981	0.010	0.998	0.017	0.012	0.993	0.012	0.012	0.993	0.012	0.000	1.000	0.019
8	0.014	0.995	0.002	1.000	0.005	0.005	0.998	0.002	0.005	0.998	0.002	0.000	1.000	0.005
9	0.000	1.000	0.000	1.000	0.000	0.002	1.000	0.000	0.000	0.998	0.002	0.000	1.000	0.000
10	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	0.998	0.002	0.000	1.000	0.000
11	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.002	1.000	0.000	0.000	1.000	0.000

Table 5

North Carolina Division of Marine Fisheries (NCDMF) 1987 bluefish (*Pomatomus saltatrix*) proportions at age (*P*) and cumulative proportions at age (*C*) compared with estimates derived by cohort slicing using NOAA (1989) parameters, by standard application of the Connecticut/New Hampshire/North Carolina age-length key (CNN ALK), the CNN age-length key applied using the iterated age-length key method (IALK), and by MULTIFAN. Maximum difference in cumulative proportions at age (*D*) in underlined bold print. $D_{0.05,\ 95}$=0.093.

Age	NCDMF *P*	NCDMF *C*	NOAA 1989 *P*	NOAA 1989 *C*	NOAA 1989 *D*	CNN ALK *P*	CNN ALK *C*	CNN ALK *D*	IALK *P*	IALK *C*	IALK *D*	MULTIFAN *P*	MULTIFAN *C*	MULTIFAN *D*
0	0.209	0.209	0.308	0.308	**0.099**	0.261	0.261	0.052	0.268	0.268	0.059	0.388	0.388	**0.179**
1	0.419	0.628	0.360	0.668	0.040	0.402	0.664	0.035	0.395	0.664	0.035	0.214	0.602	0.026
2	0.082	0.711	0.040	0.708	0.002	0.052	0.715	0.005	0.052	0.715	0.005	0.056	0.659	0.052
3	0.031	0.741	0.045	0.753	0.012	0.040	0.755	0.014	0.040	0.755	0.014	0.007	0.666	0.075
4	0.042	0.784	0.075	0.828	0.045	0.092	0.847	0.064	0.092	0.847	0.064	0.052	0.718	0.066
5	0.073	0.856	0.122	0.951	0.094	0.075	0.922	**0.066**	0.075	0.922	**0.066**	0.045	0.762	0.094
6	0.078	0.934	0.024	0.974	0.040	0.042	0.965	0.031	0.042	0.965	0.031	0.238	1.000	0.066
7	0.038	0.972	0.021	0.995	0.024	0.024	0.988	0.016	0.024	0.988	0.016	0.000	1.000	0.028
8	0.019	0.991	0.005	1.000	0.009	0.007	0.995	0.005	0.007	0.995	0.005	0.000	1.000	0.009
9	0.009	1.000	0.000	1.000	0.000	0.005	1.000	0.000	0.002	0.998	0.002	0.000	1.000	0.000
10	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	0.998	0.002	0.000	1.000	0.000
11	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.002	1.000	0.000	0.000	1.000	0.000

Table 6

North Carolina Division of Marine Fisheries (NCDMF) 1988 bluefish (*Pomatomus saltatrix*) proportions at age (*P*) and cumulative proportions at age (*C*) compared with estimates derived by cohort slicing using NOAA (1989) parameters, by standard application of the Connecticut/New Hampshire/North Carolina age-length key (CNN ALK), the CNN age-length key applied using the iterated age-length key method (IALK), and by MULTIFAN. Maximum difference in cumulative proportions at age (*D*) in underlined bold print. $D_{0.05,n=321}=0.107$.

Age	NCDMF *P*	NCDMF *C*	NOAA 1989 *P*	NOAA 1989 *C*	NOAA 1989 *D*	CNN ALK *P*	CNN ALK *C*	CNN ALK *D*	IALK *P*	IALK *C*	IALK *D*	MULTIFAN *P*	MULTIFAN *C*	MULTIFAN *D*
0	0.182	0.182	0.173	0.173	0.009	0.160	0.160	0.022	0.170	0.170	0.012	0.117	0.117	**0.065**
1	0.346	0.528	0.401	0.574	0.046	0.420	0.580	0.052	0.414	0.583	0.056	0.451	0.568	0.040
2	0.151	0.679	0.105	0.679	0.000	0.102	0.682	0.003	0.102	0.685	0.006	0.096	0.664	0.015
3	0.062	0.741	0.059	0.738	0.003	0.074	0.756	0.015	0.074	0.759	0.019	0.065	0.728	0.012
4	0.071	0.812	0.114	0.852	0.040	0.105	0.861	0.049	0.105	0.864	0.052	0.022	0.750	0.062
5	0.059	0.870	0.105	0.957	**0.086**	0.077	0.938	**0.068**	0.074	0.938	**0.068**	0.123	0.873	0.003
6	0.065	0.935	0.034	0.991	0.056	0.034	0.972	0.037	0.034	0.972	0.037	0.127	1.000	0.065
7	0.049	0.985	0.006	0.997	0.012	0.015	0.988	0.003	0.015	0.988	0.003	0.000	1.000	0.015
8	0.009	0.994	0.003	1.000	0.006	0.003	0.991	0.003	0.006	0.994	0.000	0.000	1.000	0.006
9	0.006	1.000	0.000	1.000	0.000	0.009	1.000	0.000	0.003	0.997	0.003	0.000	1.000	0.000
10	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	0.997	0.003	0.000	1.000	0.000
11	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.003	1.000	0.000	0.000	1.000	0.000

Table 7

North Carolina Division of Marine Fisheries (NCDMF) 1989 bluefish (*Pomatomus saltatrix*) proportions at age (*P*) and cumulative proportions at age (*C*) compared with estimates derived by cohort slicing using NOAA (1989) parameters, by standard application of the Connecticut/New Hampshire/North Carolina age-length key (CNN ALK), the CNN age-length key applied using the iterated age-length key method (IALK), and by MULTIFAN. Maximum difference in cumulative proportions at age (*D*) in underlined bold print. $D_{\max} = 0.111$.

Age	NCDMF *P*	NCDMF *C*	NOAA 1989 *P*	NOAA 1989 *C*	NOAA 1989 *D*	CNN ALK *P*	CNN ALK *C*	CNN ALK *D*	IALK *P*	IALK *C*	IALK *D*	MULTIFAN *P*	MULTIFAN *C*	MULTIFAN *D*
0	0.245	0.245	0.311	0.311	0.066	0.265	0.265	0.020	0.268	0.268	0.023	0.325	0.325	**0.079**
1	0.325	0.570	0.262	0.573	0.003	0.311	0.576	0.007	0.305	0.573	0.003	0.272	0.596	0.026
2	0.099	0.669	0.086	0.659	0.010	0.086	0.662	0.007	0.086	0.659	0.010	0.036	0.632	0.036
3	0.073	0.742	0.096	0.755	0.013	0.109	0.772	0.030	0.109	0.768	0.026	0.076	0.709	0.033
4	0.079	0.821	0.149	0.904	**0.083**	0.126	0.897	**0.076**	0.126	0.894	**0.073**	0.103	0.811	0.010
5	0.109	0.930	0.070	0.974	0.043	0.066	0.964	0.033	0.066	0.960	0.030	0.116	0.927	0.003
6	0.033	0.964	0.023	0.997	0.033	0.023	0.987	0.023	0.023	0.983	0.020	0.073	1.000	0.036
7	0.020	0.983	0.003	1.000	0.017	0.010	0.997	0.013	0.010	0.993	0.010	0.000	1.000	0.017
8	0.013	0.997	0.000	1.000	0.003	0.003	1.000	0.003	0.007	1.000	0.003	0.000	1.000	0.003
9	0.003	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000
10	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000
11	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.002	1.000	0.000	0.000	1.000	0.000

Table 8

North Carolina Division of Marine Fisheries (NCDMF) 1986–1989 bluefish (*Pomatomus saltatrix*) proportions at age (*P*) and cumulative proportions at age (*C*) compared with estimates derived by cohort slicing using NOAA (1989) parameters, by standard application of the Connecticut/New Hampshire/North Carolina age-length key (CNN ALK), the CNN age-length key applied using the iterated age-length key method (IALK), and by MULTIFAN. Maximum difference in cumulative proportions at age (*D*) in underlined bold print. $D_{105 \text{ in } 1989}$=0.050.

	NCDMF	NCDMF	NOAA 1989	NOAA 1989	NOAA 1989	CNN ALK	CNN ALK	CNN ALK	IALK	IALK	IALK	MULTIFAN	MULTIFAN	MULTIFAN
Age	*P*	*C*	*P*	*C*	*D*	*P*	*C*	*D*	*P*	*C*	*D*	*P*	*C*	*D*
0	0.243	0.243	0.294	0.294	0.051	0.255	0.255	0.012	0.261	0.261	0.018	0.278	0.278	0.035
1	0.386	0.629	0.365	0.659	0.030	0.404	0.658	0.029	0.398	0.658	0.029	0.357	0.635	0.006
2	0.098	0.727	0.065	0.724	0.003	0.070	0.728	0.001	0.070	0.728	0.001	0.063	0.698	0.029
3	0.041	0.768	0.050	0.775	0.007	0.058	0.786	0.018	0.058	0.786	0.018	0.034	0.732	0.035
4	0.054	0.822	0.093	0.868	0.046	0.091	0.877	**0.054**	0.091	0.877	**0.054**	0.042	0.775	**0.048**
5	0.075	0.897	0.095	0.963	**0.066**	0.067	0.944	0.047	0.067	0.943	0.046	0.083	0.858	0.039
6	0.054	0.952	0.023	0.986	0.035	0.031	0.975	0.024	0.031	0.975	0.023	0.142	1.000	0.048
7	0.028	0.980	0.011	0.997	0.018	0.016	0.991	0.012	0.016	0.990	0.011	0.000	1.000	0.020
8	0.014	0.994	0.003	1.000	0.006	0.005	0.996	0.002	0.006	0.997	0.003	0.000	1.000	0.006
9	0.006	1.000	0.000	1.000	0.000	0.004	1.000	0.000	0.001	0.998	0.002	0.000	1.000	0.000
10	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.000	0.998	0.002	0.000	1.000	0.000
11	0.000	1.000	0.000	1.000	0.000	0.000	1.000	0.000	0.002	1.000	0.000	0.000	1.000	0.000

Table 9

North Carolina Division of Marine Fisheries (NCDMF) 1986–1989 bluefish (*Pomatomus saltatrix*) annual proportions at age (P) compared with estimates derived by initial application of CNN age-length key using the iterated age-length key method (IALK). Cumulative proportions are omitted for brevity. Maximum difference in cumulative proportions at age (D) in underlined bold print. 1986 $D_{0.05,n=418}$=0.094, 1987 $D_{0.05,n=425}$=0.093, 1988 $D_{0.05,n=324}$=0.107, 1989 $D_{0.05,n=302}$=0.111.

	1986			1987			1988			1989		
Age	NCDMF P	IALK P	IALK D	NCDMF P	IALK P	IALK D	NCMDF P	IALK P	IALK D	NCMDF P	IALK P	IALK D
0	0.323	0.289	0.033	0.209	0.245	0.035	0.182	0.082	**0.099**	0.245	0.291	0.046
1	0.428	0.507	**0.045**	0.419	0.447	0.064	0.346	0.524	0.080	0.325	0.295	0.017
2	0.072	0.029	0.002	0.082	0.014	0.005	0.151	0.061	0.009	0.099	0.040	0.043
3	0.012	0.012	0.002	0.031	0.021	0.014	0.062	0.077	0.006	0.073	0.132	0.017
4	0.036	0.067	0.033	0.042	0.134	**0.078**	0.071	0.136	0.071	0.079	0.172	**0.109**
5	0.065	0.074	0.043	0.073	0.073	0.078	0.059	0.086	0.099	0.109	0.046	0.046
6	0.038	0.007	0.012	0.078	0.031	0.031	0.065	0.021	0.056	0.033	0.003	0.017
7	0.007	0.002	0.007	0.038	0.016	0.009	0.049	0.006	0.012	0.020	0.000	0.003
8	0.014	0.010	0.002	0.019	0.009	0.000	0.009	0.002	0.003	0.013	0.020	0.003
9	0.000	0.001	0.002	0.009	0.005	0.005	0.006	0.001	0.003	0.003	0.000	0.000
10	0.000	0.000	0.002	0.000	0.000	0.005	0.000	0.004	0.000	0.000	0.000	0.000
11	0.000	0.002	0.000	0.000	0.005	0.000	0.000	0.002	0.000	0.000	0.000	0.000

Table 10

Matrix of MULTIFAN inverse log-likelihood function values for alternative interpretations of the number of significant age classes underlying the North Carolina Division of Marine Fisheries 1986–1989 bluefish (*Pomatomus saltatrix*) length-frequency test data. LISD = length independent standard deviation in length at age, LDSD = length dependent standard deviation in length at age, NOSEL = no selectivity bias on the first age group, SEL = selectivity bias on the first age group. Values in parentheses are the number of parameters in model being tested (e.g., proportions at age, mean lengths at age, K, LDSD, or SEL). Bold underlined value is combination of characteristics selected for final evaluation as the best fitting model, based on the significance of increases in value with added parameters.

Ages	LISD+NOSEL	LISD+SEL	LDSD+NOSEL	LDSD+SEL
6	4171.7 (24)	4171.9 (25)	4172.4 (25)	4174.2 (26)
7	4169.9 (28)	**4180.7** (29)	4175.6 (29)	4178.4 (30)
8	4160.4 (32)	4170.0 (33)	4167.1 (33)	4168.9 (34)
9	4158.9 (36)	4169.7 (37)	4172.7 (37)	4185.8 (38)
10	4161.9 (40)	4175.7 (41)	4168.5 (41)	4187.0 (42)
11	4160.5 (44)	4171.7 (45)	4169.9 (45)	4188.1 (46)
12	4160.7 (48)	4170.3 (49)	4169.6 (49)	4187.9 (50)
13	4161.1 (52)	4170.0 (53)	4169.1 (53)	4187.8 (54)

growth follows the von Bertalanffy function. Other growth functions such as the logistic or Gomphertz may be better models of growth for the youngest age classes of fish, or for species that experience periods of rapid growth at intermediate ages followed by slow growth as they approach asymptotic sizes (Moreau, 1987; Terceiro[4]).

The normal distribution of length at age assumed in MULTIFAN is appropriate for many fish species (Fournier and Breen, 1983; Fournier et al., 1990; Terceiro et al., 1992). Other probability distributions might better describe the variation in length at age for species with special life-history characteristics. Species characterized by multiple spawning events or extreme variation in growth among cohorts due to density dependence often exhibit log-normal (long-tailed) distributions of length at age. Consideration of alternative probability distributions would be a useful addition to the MULTIFAN model. For species subject to a high degree of size selectivity within age, or those experiencing very slow growth at the oldest ages, the inclusion of parameters that account for departures from normality (skewness and kurtosis) could provide a MULTIFAN model that better estimates age from asymmetric distributions of length at age.

[4]Terceiro, M. 1991. Length composition analysis of Atlantic sea scallop using the MULTIFAN method. *In* Report of the Twelfth Northeast Regional Stock Assessment Workshop (12th SAW), Spring 1991, Appendix 1, p. 1–29. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole Lab. Ref. Doc. 91-03, 187 p.

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A statistical method for evaluating differences between age-length keys with application to Georges Bank haddock, *Melanogrammus aeglefinus*

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Age-length keys are a critical component of many methods used to estimate catch at age (Southward, 1976; Kimura, 1977; Gavaris and Gavaris, 1983; Quinn et al., 1983; Lai, 1987; Martin and Cook, 1990). When formulating age-length keys for use in stock assessment, the appropriate time interval for data collection and aggregation is an important consideration. Potentially, an age-length key derived from data taken at a single time during the year could be used to compute catch at age for the entire year. This practice runs the risk of producing inaccurate estimates of catch at age, however. Finer time intervals for age-length keys are typically used (e.g., quarterly or monthly) but at a cost of increased sampling requirements. Generally, intensive sampling over brief time intervals provides the most accurate representation of age at length in the population (Kimura, 1977; Westrheim and Ricker, 1978). In practice, however, such a strategy is expensive to implement because of the labor-intensive nature of collecting and processing large numbers of fish for age data. For the efficient and cost-effective use of sampling resources, it is desirable to sample and age the fewest fish, giving adequate precision while avoiding biased results. The data needed can be considerably reduced if appropriate time intervals for age-length keys can be defined.

A further problem facing fishery scientists is the need for evaluation of samples collected with different gears. Although fishing gears may select for fish size, the question here is whether the gears select for fish with different proportions of age at length. For example, the Northeast Fisheries Science Center (NEFSC) of the National Marine Fisheries Service samples most of the commercially important fish stocks off the northeastern United States with bottom trawls during the spring and autumn. The fish collected in these surveys have a substantially different size composition than the commercial catch because the standard survey trawl has a small mesh codend liner. However, it is unknown whether fish of a given length caught in the research survey trawl differ in age composition from fish of the same length harvested commercially. If the age at length of fish captured is the same for these gears, then a pooled key, including data from research surveys, will increase precision by increasing sample size but will not bias catch at age estimates. However, if age-length keys differ, then pooling can introduce bias into estimates of catch at age (Westrheim and Ricker, 1978).

The primary objective of this study is to present a method for determining whether two age-length keys differ statistically. This method is then applied to Georges Bank haddock to determine what time intervals should be used for age-length keys for this stock and to determine if research trawl-survey age data can be combined with age data from commercially harvested haddock. The benefit (in terms of increased precision) of pooling age-length keys, where appropriate, is also determined.

Methods

Biological sampling

Scales were collected from commercially landed haddock in the NEFSC port sampling program. Because sampling requests to this program are filled quarterly, age-length keys and the age structure of landings were computed on a quarterly basis as in previous stock assessments (Clark et al., 1982; Gavaris and Van Eeckhaute, 1990). Length at age by month was averaged over several years (1980 to 1988) to determine growth on a monthly basis. Haddock scales were also collected in the NEFSC bottom trawl research survey. The NEFSC conducts this survey during the spring and autumn each year, providing a fishery independent source of age structures. These surveys are conducted from Cape Hatteras, North Carolina, to Nova Scotia, Canada, with the use of a stratified random sampling design. Further details concerning sampling procedures in the NEFSC survey are outlined in Grosslein (1969) and Azarovitz (1981).

Scales were removed from the lateral line region below the second dorsal fin. After removal, scales were dried and then impressed on a laminated plastic slide. Scales were viewed at approximately 40× magnification to determine age. Ages were determined following cri-

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teria outlined by Penttila (1988) and Jensen and Wise (1962). By convention, a 1 January birthdate was used.

Statistical analysis

Age-length keys are commonly formed first by obtaining a matrix of numbers at age by length interval (Table 1), and then by converting this to a matrix of proportion at age for each length interval. For statistical tests between age-length keys, however, I used the matrix of numbers at age by length. Age-length keys were compared by making tests of significance separately for each length interval present in both keys where the sample size was greater than six for each age-length key. Fisher's exact test (Siegel, 1956) was used in these comparisons. Because of the large number of tests needed to compare age-length keys, experimentwise error was compensated for by adjusting the significance level for the individual tests. The significance level for n individual tests (α^*) needed to maintain a desired experimentwise error (α_{exp}) was determined by the following formula derived from Sokal and Rohlf (1981):

$$\alpha^* = 1 - e^{\frac{\ln|1-\alpha_{exp}|}{n}}$$

This method can be quite conservative if the power of the individual tests is limited because of small sample sizes (Sokal and Rohlf, 1981). Owing to the conservative nature of this method, two subjective criteria for evaluating test results were used.

The first criterion was the number of tests exceeding the nominal significance level (i.e., α=0.05) in the set of comparisons of interest. A second criterion for evaluating the significance of individual tests was the pattern of nominally significant tests. If significant differences were observed between quarters for a given length interval, adjacent length intervals were also expected to show significant differences. Thus, tests suggesting nominally significant differences between quarters for a single length interval adjacent to length intervals where tests indicate no difference were suspected of occurring by random chance.

Age-length keys from the first and second, second and third, and third and fourth quarters were compared to determine which quarters could be combined into a single age-length key. Tests were conducted by comparing keys within a year because combining age-length keys between years can introduce bias in the resulting key (Westrheim and Ricker, 1978). Additional tests were conducted comparing NEFSC spring survey age-length keys with combined first and second quarter commercial age-length keys.

Table 1

Number sampled at age by 2-cm length groups from the commercial catch of Georges Bank haddock *Melanogrammus aeglefinus*, January to March 1983.

	Age								
Length (cm)	2	3	4	5	6	7	8	9+	Total
42	1	2	0	0	0	0	0	0	3
44	0	6	0	0	0	0	0	0	6
46	0	4	2	0	0	0	0	0	6
48	0	4	1	1	0	0	0	0	6
50	0	3	5	4	0	0	0	0	12
52	0	2	5	6	1	0	0	0	14
54	0	1	8	14	0	0	0	0	23
56	0	0	9	11	0	0	0	0	20
58	0	0	5	12	1	0	0	0	18
60	0	0	3	8	2	0	6	0	19
62	0	0	3	8	4	0	6	0	21
64	0	0	0	12	3	1	2	1	19
66	0	0	0	9	3	0	7	0	19
68	0	0	0	8	0	0	6	1	15
70	0	0	0	4	1	4	8	0	17
72	0	0	0	0	1	3	9	0	13
74	0	0	0	2	0	2	10	1	15
76	0	0	0	0	1	1	9	0	11
78	0	0	0	0	1	1	6	1	9
80	0	0	0	0	0	1	7	1	9
82	0	0	0	0	0	0	7	1	8
84	0	0	0	0	0	0	1	1	2
86	0	0	0	0	0	0	1	0	1

Estimation of catch at age and variance

As a check on the potential for introducing bias by combining age-length keys, estimates of the age composition of the commercial catch for each year from 1982 to 1988 were made by using age-length keys combined in four different ways. First, age-length keys were constructed for each quarter by using only fish sampled commercially during that quarter. These catch-at-age estimates served as a basis for comparison since they correspond to the level of temporal aggregation (quarterly) that has commonly been used in Georges Bank haddock assessments (Clark et al., 1982; Gavaris and Van Eeckhaute, 1990). The second set of catch-at-age estimates was formed by combining commercial age data from the first half of the year into a single age-length key that was then applied to the first and second quar-

ter length-frequency distributions. The third set of catch-at-age estimates was based on quarterly age-length keys but included data from haddock sampled in the commercial catch and from the NEFSC bottom trawl surveys. The final set of age-length keys contained data from haddock caught both commercially and in trawl surveys but combined all data for the first half of the year.

I treated length-frequency samples as simple random samples from the entire stock area in the computation of the variance of catch at age. Following Gavaris and Gavaris (1983), the proportion of catch at age for unpooled samples was estimated as

$$\hat{A}_{iq} = \sum_{j} L_{jq} P_{ijq}$$

where,

$\hat{A}_{iq}$ = Estimated proportion at age i in quarter q
L_{jq} = Proportion of total individuals at length j in quarter q
P_{ijq} = Proportion of age i individuals at length j in quarter q.

For samples where age-length keys were pooled across quarters, the proportion of catch at age was estimated as

$$\hat{A}_{iq} = \sum_{j} L^{*}_{jq} P^{*}_{ijq}$$

where P^{*}_{ijq} is the proportion of age i individuals at length j for the pooled quarters, and L^{*}_{jq} is the pooled proportion at length j in the pooled quarters. These proportions were calculated as

$$P^{*}_{ijq} = \frac{n_{ij1} + n_{ij2}}{n_{j1} + n_{j2}},$$

$$L^{*}_{jq} = \frac{(L_{j1})N_1 + (L_{j2})N_2}{N_1 + N_2},$$

where,

n_{ij1} = # of age i fish at length j in first time period
n_{ij2} = # of age i fish at length j in second time period
n_{j1} = # of fish at length j in first time period
n_{j2} = # of fish at length j in second time period
N_1 = total # of fish landed in first time period
N_2 = total # of fish landed in second time period.

This method of pooling age-length keys treats each observation as a random sample from a single population. No weighting factors were applied when age-length keys were pooled. A pooled proportion of total individuals at length was computed as a stratified random sample where the weighting for each quarter was the total number of individuals landed during that period. This allows for the possibility that the length composition of landings differed between quarters.

Estimates of the variance of proportion at age for unpooled data were computed following Gavaris and Gavaris (1983):

$$\mathrm{Var}\,(\hat{A}_{iq}) = \sum_{j} \frac{L^{2}_{jq} P_{ijq}(1-P_{ijq})}{n_{jq} - 1} + \frac{L_{jq}(P_{ijq} - \hat{A}_{iq})^{2}}{n_{q}}$$

Where n_q is the number of fish aged in quarter q.

Estimates of the variance of proportion at age when age-length keys were pooled were computed with the above formulae, except P^{*}_{ijq} was substituted for P_{ijq}. Catch at age and variance for each quarter were computed following Gavaris and Gavaris (1983). Because these computations do not depend on whether pooled or unpooled age-length keys are used, the formulae are not repeated.

Results and discussion

Seasonal growth and comparison of age-length keys

Most of the annual growth of Georges Bank haddock takes place during the third quarter, from June through September (Fig. 1). From this pattern of annual growth, age-length keys would not be significantly different between the first and second quarters, but would differ significantly betweens the second and third quarters, and the third and fourth quarters. Accordingly, tests were conducted between these pairs of quarters to determine if age-length keys could be pooled across any adjacent quarters. Summary statistics of these tests are presented in Tables 2 through 4. Although little growth takes place between the fourth quarter and the first quarter in the following year, landings data are usually finalized on an annual basis; pooling between years is therefore of limited use.

Comparisons between the first and second quarters yielded 9 of 94 tests exceeding the 0.05 level (Table 2). None of these tests exceeded the adjusted significance level (α^{*}=0.00054) needed to maintain an error rate of 0.05 for this set of comparisons. The number of results exceeding 0.05 is not substantially greater than the number of significant results that would be expected based on random chance; further, these differences occurred sporadically among the length classes (Table 2). Thus, based on these tests, first and second quarter age-length keys within each year can be treated as samples drawn from the same population and can be pooled.

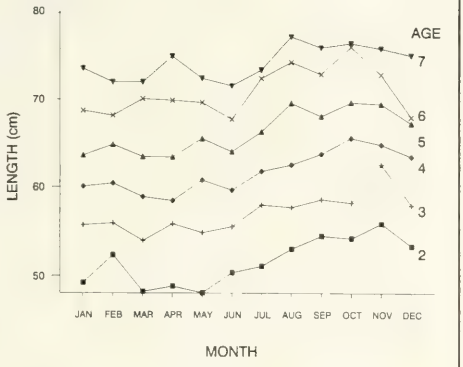

Figure 1
Monthly mean length at age of Georges Bank haddock *Melanogrammus aeglefinus* in the commercial catch, 1980–1988.

Significant differences were observed between second and third quarter age-length keys; 45 of 95 comparisons exceeded the 0.05 level, and 19 tests of these tests had probabilities of less than 0.00054 (α^*) (Table 3). Tests between the third and fourth were not as definitive; 21 of 85 comparisons exceeded the 0.05 level, but no tests exceeded 0.00060 (α^*). Several tests, however, were close to α^* (Table 4). The large number of tests exceeding 0.05 and the occurrence of contiguous blocks of tests with low probability (Table 4) indicate that age-length keys differ between the third and fourth quarters, but the power to detect these differences may have been limited by small sample sizes. In general, the number of fish aged from the fourth quarter was lower than those from other quarters as indicated by the smaller number of length intervals with sample sizes greater than six. From these results, age-length keys should not be combined across the second and third quarters or third and fourth quarters for haddock. The consequence of pooling age-length keys across quarters when statistical tests indicate significant differences would be to bias catch-at-age estimates (Westrheim and Ricker, 1978). In the case of Georges Bank haddock, the effect of pooling third quarter age-length keys with second quarter keys (for example) would be to bias catch-at-age estimates for the second quarter towards younger fish. This occurs because growth during the third quarter tends to increase the mean length at age, and conversely, fish of a given length tend to be younger during the third quarter than during the second quarter.

Comparison of pooled first and second quarter age-length keys with spring NEFSC bottom trawl surveys keys resulted in 7 of 71 tests having probabilities less than 0.05 (Table 5), but none exceeding the α^* level of 0.00072. Although more "significant" results were obtained than would be expected by random chance, no consistent pattern among these differences was apparent (Table 5). Further, several of these differences occurred in the 60 to 66 cm size classes where the sample size from the bottom trawl survey was generally small (<10 fish), while sample sizes from the commercial catch were often large (>50 fish). Examination of the contingency tables for these size classes indicated that the difference in proportion at age between commercial and survey age-length keys was small and was often due to a broader representation of age classes in the commercial data. A broader representation in the commercial samples would be expected, however, given the

Table 2
Results of Fisher's exact test comparing first and second quarter age-length keys from Georges Bank haddock *Melanogrammus aeglefinus*, 1982–1988. Entries are probability of difference observed occurring by random chance. Dashes indicate comparisons where the sample size was less than seven within one of the two quarters being compared.

Length (cm)	Year						
	1982	1983	1984	1985	1986	1987	1988
42	—	—	—	—	—	—	—
44	0.307	0.676	—	—	—	—	—
46	0.782	0.117	0.559	1.000	—	—	—
48	1.000	0.804	0.892	0.661	—	—	1.000
50	0.888	0.033*	0.653	0.289	—	—	—
52	0.786	0.819	0.022*	0.363	—	—	0.724
54	0.176	0.434	0.143	0.008*	—	0.018*	0.026*
56	0.051	0.284	0.207	0.451	—	1.000	0.067
58	0.562	0.749	0.002*	0.074	0.753	0.434	0.744
60	0.177	0.002*	0.950	0.889	0.432	0.303	0.870
62	0.153	0.123	0.163	—	1.000	0.799	0.406
64	0.136	0.372	0.223	—	0.644	0.389	0.464
66	0.300	0.694	0.849	—	0.230	0.950	0.811
68	0.352	0.497	0.373	—	0.418	0.461	0.704
70	0.182	0.032*	0.676	—	1.000	1.000	0.799
72	0.097	0.119	0.584	—	0.143	1.000	0.439
74	0.730	0.808	0.036*	—	0.128	—	—
76	0.488	0.589	0.096	—	—	—	—
78	—	0.852	0.249	—	—	—	—
80	—	1.000	0.161	—	—	—	—
82	—	0.466	—	—	—	—	—

*$P<0.05$

Table 3

Results of Fisher's exact test comparing second and third quarter age-length keys from Georges Bank haddock *Melanogrammus aeglefinus*, 1982–1988. Entries are probability of difference observed occurring by random chance. Dashes indicate comparisons where the sample size was less than seven within one of the two quarters being compared.

Length (cm)	Year						
	1982	1983	1984	1985	1986	1987	1988
42	0.219	0.170	—	—	—	—	—
44	<0.001**	0.075	—	0.592	—	—	—
46	<0.001**	0.017*	—	0.020*	—	—	—
48	<0.001**	0.110	0.620	0.013*	—	<0.001**	0.832
50	<0.001**	0.026*	0.747	0.108	—	<0.001**	0.773
52	<0.001**	<0.001**	1.000	0.115	1.000	0.003*	<0.001**
54	<0.001**	<0.001**	0.688	0.011*	0.582	0.012*	<0.001**
56	0.042*	<0.001**	1.000	0.321	0.429	0.488	<0.001**
58	0.046*	<0.001**	0.146	0.053	0.115	0.335	<0.001**
60	0.038*	<0.001**	0.863	—	<0.001**	0.075	<0.001**
62	0.011*	0.011*	0.106	—	0.002*	0.055	<0.001**
64	0.523	0.015*	0.662	—	0.004*	0.010*	—
66	0.246	0.032*	0.354	—	0.292	0.004*	—
68	0.068	0.016*	0.192	—	0.046*	0.122	—
70	0.544	0.002*	0.700	—	0.011*	0.046*	—
72	0.379	0.022*	0.738	—	0.590	0.058	—
74	0.185	0.544	—	—	0.020*	0.755	—
76	0.686	0.407	—	—	0.569	—	—
78	—	0.427	—	—	—	—	—
80	—	0.206	—	—	—	—	—
82	—	0.537	—	—	—	—	—

*$P<0.05$
**$P<0.00054=\alpha^*$

Table 4

Results of Fisher's exact test comparing third and fourth quarter age-length keys from Georges Bank haddock *Melanogrammus aeglefinus*, 1982–1988. Entries are probability of difference observed occurring by random chance. Dashes indicate comparisons where the sample size was less than seven within one of the two quarters being compared.

Length (cm)	Year						
	1982	1983	1984	1985	1986	1987	1988
42	0.286	1.000	—	—	—	—	—
44	0.298	0.014*	—	—	—	—	—
46	0.158	0.003*	—	—	—	1.000	—
48	0.051	0.001*	—	—	—	0.192	0.124
50	<0.001*	0.123	0.123	—	—	0.053	1.000
52	0.159	0.315	0.212	—	—	0.024*	0.832
54	0.146	0.049*	0.720	—	—	0.754	0.211
56	0.205	0.765	1.000	—	—	0.050*	0.791
58	0.143	0.009*	0.154	—	0.477	0.675	0.016*
60	0.292	0.174	0.939	—	0.794	0.540	0.014*
62	0.028*	0.032*	0.758	—	0.272	0.244	<0.001*
64	0.265	0.042*	0.132	—	0.085	0.022*	—
66	0.014*	0.034*	0.079	—	0.785	<0.001*	—
68	0.484	0.937	0.759	—	0.068	0.107	—
70	0.011*	0.038*	0.218	—	0.207	0.046*	—
72	1.000	0.813	0.550	—	1.000	0.408	—
74	0.756	0.162	—	—	0.054	0.922	—
76	0.282	0.612	—	—	0.713	—	—
78	0.355	0.499	—	—	1.000	—	—
80	0.765	—	—	—	—	—	—
82	—	—	—	—	—	—	—

*$P<0.05$

larger sample size available from the commercial fishery for fish in these length classes. Based on the lack of pattern among the significance tests and the lack of tests exceeding α^*, it appears that survey gear does not more consistently select for fish of a different age at a given length than do commercial fishing gears. Accordingly data on age at length obtained from fish collected in the research surveys can be combined with data from fish sampled commercially.

Catch at age and precision

Catch-at-age estimates obtained with the various age-length keys showed no indication of systematic bias (Fig. 2). This was expected, as the results of statistical tests indicated no significant difference between the age-length keys that were pooled. The precision of catch-at-age estimates, however, did show a trend among the different levels of aggregation (Fig. 3). Combining first and second quarter age-length keys derived solely from commercially caught haddock increased precision for all age groups, particularly for older age classes that typically had small sample sizes within a single quarter (e.g., the 82 and 84 cm length classes; Table 1). The inclusion of survey age data had a relatively smaller effect on the precision of estimates for most age classes except for age-2 fish (Fig. 3). This occurred because the sample size of small haddock was generally less in the commercial samples than in the research survey samples.

Statistical considerations

Fisher's exact test tests the hypothesis that the proportion at age within each length class is no different among keys than would be obtained by random chance.

Formally, the hypothesis tested

for length class j is

Ho: $p_{ij1} = p_{ij2}$ for all age classes i from source 1 and source 2

Ha: $p_{ij1} \neq p_{ij2}$ for all age classes i from source 1 and source 2.

Consider as an example haddock (*Melanogrammus aeglefinus*) in the 54-cm size class sampled from the commercial catch from the first and second quarters of 1983. Numbers at age from each of these samples are

	Age									
	0	1	2	3	4	5	6	7	8	Total
Quarter 1	0	0	0	1	8	14	0	0	0	23
Quarter 2	0	0	0	7	10	24	1	0	0	42

The question asked is whether the two samples are likely to be drawn from the same population or whether they differ sufficiently to indicate that the sampled populations are different. Assuming fixed marginal totals, an appropriate test of this hypothesis is Fisher's exact test (Siegel, 1956). Previously this test was impractical for contingency tables greater than 2 × 2 because of the amount of computational power required by the algorithms available for its solution. Recent improvements (Pagano and Halvorsen, 1981; Mehta and Patel, 1983; implemented in Version 6 of SAS [SAS Institute, 1990]) allow problems of this size to be readily solved.

Alternative tests exist in the chi-square test of homogeneity (Hennemuth, 1965) and the G^2 test (Bishop et al., 1975). These tests have the advantage that age-length keys can be compared in their entirety. Some studies indicate that these tests may also have greater power than Fisher's exact test (D'Agostino et al., 1988; Storer and Kim, 1990), but others have disputed the validity of this these assertions (Little, 1989). Also, the chi-square and G^2 tests are often viewed as inappropriate when some of the expected values are less than 5 (e.g., Sokal and Rohlf, 1981; Haberman, 1988); a situation that commonly occurs in comparisons of age-length keys. Although grouping data across age or length classes is a way of increasing the expected values for each cell in the contingency table, such a procedure results in a loss of statistical power (Cochran, 1952).

With Fisher's exact test, there are no restrictions on the expected values for any cell within the contingency table (Siegel, 1956). In practice, however, each source (i.e., time period) should contain at least six observations because smaller sample sizes do not have sufficient power to resolve even major discrepancies between sources (Bennett and Hsu, 1960).

In summary, Fisher's exact test provides a means of testing differences between age-length keys derived from different sources or from different time periods. When age-length keys are pooled across time periods or sources that do not differ significantly, the resulting estimates of catch at age are more precise and importantly do not appear to be biased by the pooling procedure. For Georges Bank haddock, age-length keys from commercially harvested haddock from the first and second quarters can be combined, as well as keys from haddock sampled in the NEFSC research survey. In the future, allocation of sampling effort should consider the benefits of pooling age-length keys.

Acknowledgments

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Table 5

Results of Fisher's exact test comparing age-length keys for Georges Bank haddock *Melanogrammus aeglefinus* derived from fish sampled in NEFSC bottom trawl surveys to commercially sampled fish from the first and second quarters, 1982–1988. Entries are probability of difference observed occurring by random chance. Dashes indicate comparisons where the sample size was less than seven within one of the two sources being compared.

Length (cm)	Year						
	1982	1983	1984	1985	1986	1987	1988
38	0.209	—	—	—	—	—	—
40	0.214	—	—	—	—	—	—
42	—	—	0.054	—	0.350	—	—
44	—	—	0.151	—	1.000	—	—
46	0.087	—	—	0.699	0.232	—	1.000
48	0.038*	1.000	—	—	0.243	—	1.000
50	0.388	1.000	0.344	—	0.095	—	—
52	0.151	0.175	—	—	0.220	0.241	—
54	0.107	0.479	0.547	0.123	—	0.360	—
56	0.002*	0.014*	0.146	0.093	0.033*	0.465	1.000
58	0.139	0.127	0.057	0.549	—	—	—
60	0.019*	0.839	1.000	0.102	0.273	—	—
62	0.268	0.470	0.554	0.165	0.179	0.079	—
64	—	0.526	0.163	0.391	0.641	0.302	—
66	0.821	0.302	0.026*	0.768	0.003	—	—
68	—	0.191	0.128	0.725	—	—	—
70	0.625	0.139	0.423	0.745	—	—	—
72	0.777	0.682	—	—	—	—	—
74	—	—	—	0.066	—	—	—
76	0.927	0.194	—	—	—	—	—

*$P<0.05$

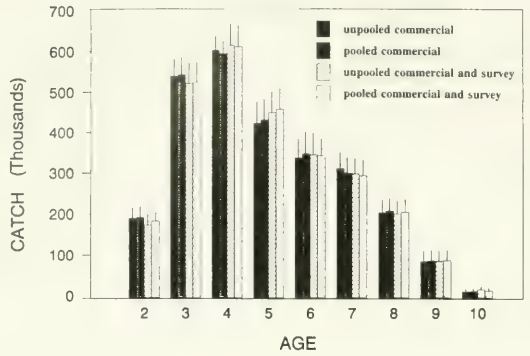

Figure 2

Mean catch at age of Georges Bank haddock *Melanogrammus aeglefinus*, 1982–1988, based on different levels of aggregation in the age-length key. Unpooled commercial refers to quarterly age-length keys derived solely from commercial samples. Pooled commercial refers to age-length keys derived solely from commercial samples, but with quarter-1 and quarter-2 data pooled into a single age-length key. Pooled and unpooled commercial and survey refer to the same levels of temporal aggregation as above but include age-at-length data obtained from fish collected in the NEFSC bottom trawl surveys. Vertical lines indicate 2 SE of the mean catch at age.

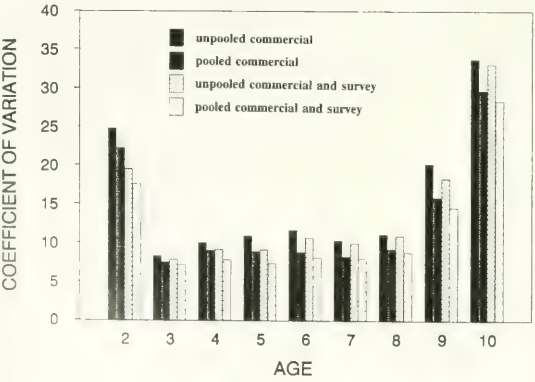

Figure 3

Mean coefficient of variation of estimates of catch at age for Georges Bank haddock *Melanogrammus aeglefinus*, 1982–1988, based on different levels of aggregation in the age-length key. Symbol definitions as in Figure 2.

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Direct validation of black drum (*Pogonias cromis*) ages determined from scales

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In the 1980's increased harvest of black drum (*Pogonias cromis*) in the Gulf of Mexico raised concerns about the possibility of overfishing (Anonymous[1]; Murphy and Taylor, 1989). Growth information necessary to examine the effects of fishing on population size was limited to rate estimates based primarily on temporal changes in length-frequency distributions (Pearson, 1929; Simmons and Breuer, 1962) and length changes in recaptured tagged fish (Osburn et al., 1980; Doerzbacher et al., 1988). Age information was limited to scale analysis of fish in Texas and Virginia (Pearson, 1929; Richards, 1973). Consequently, scales and otoliths became the focus of study for estimating age and growth rates (Cornelius, 1984; Music and Pafford, 1984; Murphy and Taylor, 1989; Beckman et al., 1990; Peters and McMichael, 1990), but, age data were not directly validated. For example, Beckman et al. (1990) used the intra-year progression of annulus formation on otoliths to conclude that one annulus forms per year. While their indirect evidence is compelling, age was not directly validated, and no attempt has been made to validate age by using the scale method. Thus, the reliability of conclusions concerning the effect of fishing on black drum may be suspect. More cost-efficient studies would result from using scales instead of otoliths for ageing if reliable data could be obtained from scales. The objectives of this study were to validate directly the formation of annuli (one growth check per year) on scales, the time of annulus formation, and the effect of tagging on annulus formation.

Methods

Black drum were caught in gill nets at randomly selected sites in nine Texas bay systems (Dailey et al., 1991) during spring (April–June) and fall (Sept.–Nov.) 1985–1991. Captured fish were measured for total length (TL) to the nearest mm, tagged with internal abdominal tags with external plastic streamers (Osburn et al., 1980), and released. Prior to release, at least two scales were removed from the area beneath the distal end of the left pectoral fin immediately ventral to the lateral line (Matlock et al., 1987). Scales were removed from a total of 9,088 released tagged black drum (195–1,257 mm TL) between April 1985 and December 1991. Anyone capturing a tagged fish was requested through posters and news-media advertisements to report date, location, and TL of each recaptured tagged fish, and to return at least one scale collected from the same area from which scales were removed at release. Scales from 22 recaptured tagged fish (354–635 mm TL) were returned to the Texas Parks and Wildlife Department (TPWD) by fishermen between May 1985 and December 1991. All reported data were assumed accurate.

Scales were prepared by washing in soapy water and impressing on a cellulose acetate slide with a roller press (Smith, 1954). The impressions were examined at 32 diameters magnification with a microprojector by using incandescent light. Annuli, characterized by breaks in circuli and new radii, were identified following Pearson's (1929) description and separately counted by two examiners without collaboration. Scales were read blind (i.e., without knowing TL or date each scale was obtained). Agreement between readers was obtained for all scales on the first reading. Scale radii and distances from the focus to successive annuli were measured along a diagonal line (Fig. 1) to the right antero-lateral scale corner (Klima and Tabb, 1959). Magnified (32×) scale measurements are reported unless otherwise noted. Sixteen of the 22 fish had both usable scales and TL measurements at both release and recapture; 17 had usable scales at both times but one fish lacked TL data at recapture (Table 1). The usable data from the remaining five fish were used to accomplish some of the objectives.

Annulus formation was validated by comparing the number of scale growth checks observed at release to those at recapture (Fig. 2). The difference in number of annuli was compared to the expected difference under the null hypothesis: number of scale growth checks per year ≠ 1.

[1]Anonymous. 1989. Saltwater finfish research and management in Texas: a report to the Governor and the 71st Legislature. Tex. Parks Wildl. Dep., PWD R-3400-061-12/88, Austin, TX, 65 p.

Manuscript accepted 24 June 1993.
Fishery Bulletin: 91:558-563 (1993).

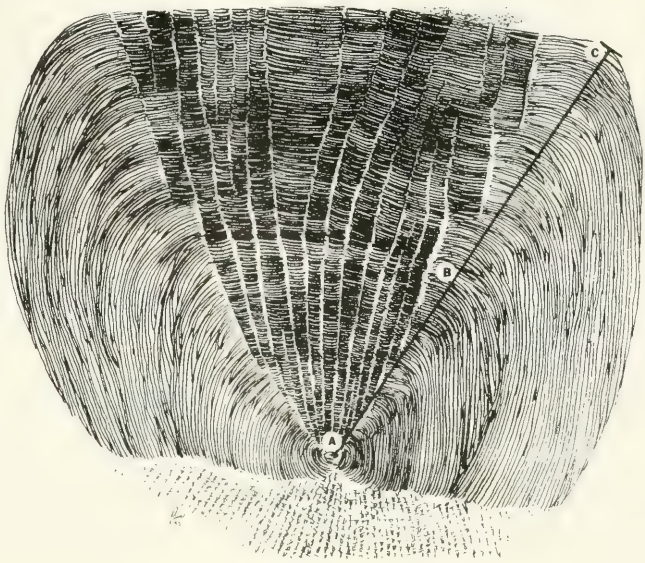

Figure 1
Black drum scale indicating morphological features used to measure radii and annuli: A = focus, B = annulus, and C = scale margin.

The time of annulus formation was estimated by narrowing the possible time(s) using the fish with increased numbers of scale annuli. The longest period between release and recapture defined the possible period of formation. This estimate was refined by using the fish free the next longest period, and so on. Fish with no annuli increases were then used to confirm or refine the possible period of annulus formation.

The effect of tagging on scale growth was examined by comparing the relationship between scale radius (Y) and total length (X) and the mean distances from scale focus to each annulus at release to those at recapture. Least-squares linear regression for single Y at each X and analysis of covariance (Sokal and Rohlf, 1981) were used to compare relationships. One-way analysis of variance (Sokal and Rohlf, 1981) was used to compare distances from focus to each of the first three annuli. The lack of scales with more than three annuli at release precluded comparison of other annuli. The probability level for all statistical analyses was set at 0.05.

Results and discussion

The scale method for aging black drum <4 years old is valid. Only one opaque zone was formed each year, between April and May. Eight of the 17 fish with usable scales at release and recapture had scales with more annuli (1) at recapture than at release (Table 1). All fish except one (B71764) were free during May; the one exception was free through 21 April. This suggests that annulus formation is completed between late April and late May. Data from the five fish not free during April or May support this conclusion; the number of annuli did not increase between release and recapture. Two fish free for 1 day in May provided little information; both showed no change in number of annuli. Two other fish released in late April and early May did not show an increase in number of annuli. One fish (F31261) released in late April may have formed an annulus just prior to initial capture, since the second annulus was located 154 mm from the scale focus, and the scale radius was 163 mm (Table 1).

Table 1

Release and recapture data for each black drum tagged in Texas bays during April 1985 through December 1991.

Tag No.	When measured[1]	Date	Bay system	Total length (mm)	Scale radius[2] (mm)	Distance (mm) to annulus 1	2	3	4	5
B71575	Release	10-28-86	Aransas	388	155	60				
	Recapture	06-26-87	Aransas	471	192	65	160			
B71764	Release	10-28-87	Aransas	533	181	63	92	133		
	Recapture	04-21-88	Aransas	522	227	69	108	183	213	
F21080	Recapture	05-02-85	Galveston	468	186	75	153	170		
F24845	Release	10-02-85	Lower Laguna Madre	548	210	65	130	160		
	Recapture	01-07-86	Lower Laguna Madre	555	200	55	100	165		
F24355	Recapture	04-29-86	Lower Laguna Madre	635	219	62	91	156	172	201
F27341	Release	04-18-89	East Matagorda	463	174	71	169			
	Recapture	10-16-90	East Matagorda	632	245	78	172	213		
F27765	Release	05-30-90	East Matagorda	507	200	78	174			
	Recapture	12-02-90	Gulf of Mexico	554	219	85	180	208		
F28057	Recapture	09-10-85	Matagorda	558	250	145	172	210		
F28641	Recapture	11-16-87	Matagorda	572	177	111	150			
F28988	Release	10-22-87	Matagorda	485	200	85	130			
	Recapture	01-18-89	Gulf of Mexico	620	230	80	115	183		
F29119	Release	05-03-88	Matagorda	418	172	63	127	156		
	Recapture	03-14-90	Matagorda	610	204	71	134	175	194	
F29583	Release	10-24-89	Matagorda	343	136	54				
	Recapture	05-24-90	San Antonio	441	142	54	113			
F29867	Release	05-09-90	Matagorda	374	151	61	128			
	Recapture	08-14-90	Matagorda	384	165	81	134	160		
F31261	Release	04-27-89	Corpus Christi	444	163	74	154			
	Recapture	03-07-90	Corpus Christi	526	218	88	179			
F31642	Release	10-25-89	Corpus Christi	511	194	73	150			
	Recapture	12-15-89	Corpus Christi	Not provided	210	65	157			
F31801	Release	05-02-90	Corpus Christi	484	181	82	180			
	Recapture	01-22-91	Corpus Christi	457	143	80	118			
F34101	Release	10-08-87	Galveston	370	124	62				
	Recapture	02-12-88	Galveston	354	135	66				
F37668	Release	05-22-90	Upper Laguna Madre	417	161	68	158			
	Recapture	05-23-90	Upper Laguna Madre	417	161	63	158			
F37671	Release	05-22-90	Upper Laguna Madre	417	158	65	153			
	Recapture	05-23-90	Upper Laguna Madre	417	164	62	159			
F42134	Release	06-01-88	San Antonio	468	164	65	103	140		
	Recapture	12-02-88	San Antonio	584	232	65	154	210		
F42489	Release	09-28-89	San Antonio	398	155	79	116			
	Recapture	01-29-90	Aransas	438	173	81	138			
F71439	Recapture	10-28-86	Aransas	560	253	90	185	215		

[1] Data from all fish with TL measured at release were used to estimate scale radius-TL relationship at release in Table 2; data from all fish measured at recapture (excludes tag F31642) were used to estimate scale radius-TL relationship at recapture in Table 2. All scale radius and TL data in this table (except recapture data for tag F31642) were used to estimate the "combined" regression in Table 2.

[2] 32 × magnification.

Tagging did not appear to influence scale growth or annulus formation, based on scale radius-TL relationship, mean distance from focus to annuli, and similar research with a related sciaenid, red drum (*Sciaenops ocellatus*). The relationship between scale radius and TL (Table 2, Fig. 3) at release was not significantly different from that at recapture (slopes: F=0.14, df=1,34; P=0.80; y-intercepts: F=0.37; df=1,35; P=0.80). The regression for all data combined explained 74% of the variation (r=0.86) and indicated scale radius increased 0.36 unit for each unit of TL increase (Table 2).

Distance of each of the first two annuli from scale focus at release was not significantly different from that at recapture (first annulus: F=2.437; df=1,37; P=0.14; second annulus: F=0.179; df=1,33, P=0.63). However, the mean distance from scale focus to the third annulus was significantly (F=11.078; df=1,14; P=0.005) greater on scales from fish at recapture

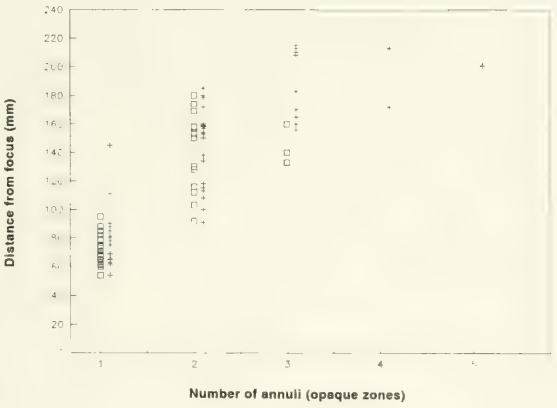

Figure 2
Scale radius distance (32× magnification) to each successive annulus on tagged black drum at release (squares) and at recapture (+).

(187 ± 7 mm) than on those from fish at release (147 ± 4 mm). The difference was due largely to small sample size; a third annulus occurred at 133 mm on one fish (B71764) at release but at 183 mm at recapture (Table 1). The same tagging procedures we used for black drum were used for red drum without affecting scale growth or annulus formation (Matlock et al., 1987). Annuli on black drum scales were formed at mean distances from scale focus (± 1 SE) of 73 ± 3 mm, 143 ± 5 mm, 179 ± 8 mm, 192 ± 20 mm, and 201 mm (Table 3).

The assumption that fishermen reported TL accurately appears valid, but they apparently reported TL less precisely than did TPWD personnel. Evidence for this is that the 95% confidence interval associated with the scale radius-TL relationship was wider for recapture data than for release data (Table 2), but the regressions were not significantly different from each other. Ferguson et al. (1984) demonstrated that anglers in Texas generally report accurate length of recaptured tagged fish, although length measurement reported by anglers were less precise than TPWD measurements for the same fish.

The life history of black drum and annulus formation in related sciaenids further support that black drum scale annulus formation is completed during April and May. Adult black drum spawn during January through April; peak spawning is in March or April (Murphy and Taylor, 1989). Growth in TL is continuous until water temperature cools in winter (December through February) when growth slows substantially (Doerzbacher et al., 1988). Growth increases in spring. If scale growth follows a similar pattern, circuli are closer to each other as growth increases after winter (i.e., annulus formation is completed in spring). Red drum (>1-year-old) growth pattern is similar to black drum and circuli deposition on red drum scales (annulus formation) occurs as expected (Colura et al., 1984; Matlock et al., 1987; Doerzbacher et al., 1988; Green et al., 1990; Bumgaurdner, 1991). If annulus formation in all black drum bony structures (e.g., scales and otoliths) occurs at the same time, then indirect evidence of annulus formation in black drum otoliths also supports the formation of annuli between April and June (Bechman et al., 1990). Additional research is needed to validate annulus formation on scales with four or more annuli.

Acknowledgments

We thank the staff of the Texas Parks and Wildlife Department, Coastal Fisheries Branch, who removed scales from black drum at tagging and David Pina for preparing the final drawing of a black drum scale. We also appreciate two anonymous reviewers and Ronald Hardy who provided constructive comments and suggestions that improved the clarity of the manuscript.

Table 2
Regression statistics for scale radius (Y in mm × 32× magnification)—total body length (X in mm) relationships ($Y = a + bX$) for scales taken from tagged black drum released and recaptured in Texas bays during April 1985 through December 1991. See Table 1 for which fish were used in each analysis.

Time measurements recorded	No. fish measured	a	b	95% CI around b	r	F
Release	17	15.85	0.34	0.26–0.42	0.905**	58.38**
Recapture	21	17.17	0.35	0.24–0.50	0.807**	35.20**
Combined	38	11.44	0.36	0.29–0.45	0.860**	105.33**

**P<0.01.

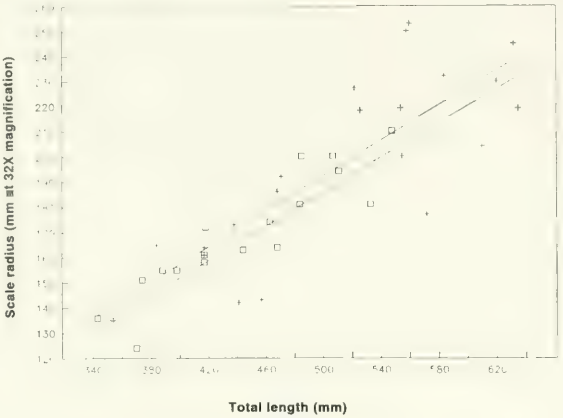

Figure 3

Relationship between fish TL and scale radius (32× magnification) for tagged black drum at release (squares, and bottom line) and at recapture (+, and top line).

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Table 3

Mean (±1SE) distance (mm at 32× magnification) from focus to annulus (*Y*) for each annulus on scales taken from black drum tagged and recaptured in Texas bays during April 1985 through December 1991.

Time measurements recorded	No. scales measured	Mean distance to annulus (number of annuli measured) 1	2	3	4	5
Release	17	[1]69±2 (17)	[4]140±7 (14)	[3]147±4 (4)		
Recapture	22	[1]77±4 (22)	[5]144±6 (21)	[6]187±7 (12)	192±20 (2)	[8]201 (1)
Combined	39	[1,4]73±3 (39)	[2,5]143±5 (35)	[3,6]179±8 (16)	[7]192±20 (2)	[8]201 (1)

[1] Tagged fish used in analysis were B71575, B71764, F24845, F27341, F27765, F28988, F29119, F29583, F29867, F31261, F31642, F31801, F34101, F37668, F37671, F42134, and F42489.

[2] Tagged fish used in analysis were the same as in footnote 1 except B71575, F29583, and F34101.

[3] Tagged fish used in analysis were B71764, F24845, F29119, and F42134.

[4] Tagged fish used in analysis were B71575, B71764, F21080, F24845, F24355, F27341, F27765, F28057, F28641, F28988, F29119, F29583, F29867, F31261, F31642, F31801, F34101, F37668, F37671, F42134, F42489, and F71439.

[5] Tagged fish used in analysis were the same as in footnote 4 except F34101.

[6] Tagged fish used in analysis were B71764, F21080, F24845, F24355, F27341, F27765, F28057, F28988, F29119, F29867, F42134, and F71439.

[7] Tagged fish used in analysis were B71764 and F24355.

[8] Tagged fish used in analysis was F24355.

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Incorporation of between-haul variation using bootstrapping and nonparametric estimation of selection curves.

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The most frequently used parametric description of trawl selectivity is the logistic curve. If $r(l)$ denotes the retention probability of a length l individual, the logistic selection curve is specified as

$$r(l) = \frac{\exp(a + bl)}{1 + \exp(a + bl)}, \quad (1)$$

where a and b are parameters to be estimated. Under this formulation it can be seen that $b>0$, because this is a requirement for $r(l)$ to increase with l. Also, $a<0$ because we require the retention probability of a length-0 individual to be (effectively) zero. A similar curve is provided by the probit function (the cumulative distribution function of the Normal distribution) which has slightly shorter tails than the logistic curve (McCullagh and Nelder, 1989). Both of these curves are symmetric about the length at which retention is 50%, which will be denoted by l_{50}. More generally, l_x will denote the length at which retention is x%.

Some selectivity data suggest an asymmetric selection curve. The log-log curve (also known as the Gompertz curve) and complimentary log-log curve are two parameter asymmetric curves that can be used in the analysis of count data (McCullagh and Nelder, 1989). Although Pope et al. (1975) mention the log-log curve as a potential selection curve, neither of these asymmetric curves appears to have been used in published selectivity studies prior to this current study.

Richards curves (Richards, 1959) are three parameter curves that generalize the logistic in the form

$$r(l) = \left(\frac{\exp(a + bl)}{1 + \exp(a + bl)}\right)^{1/\delta}. \quad (2)$$

Parameter δ controls the amount of asymmetry with $\delta>1$ or $0<\delta<1$ giving longer tail to the left or right of l_{50} respectively, and $\delta=1$ giving the symmetric logistic curve. The author (Millar, 1991) has found that the Richards curve will often provide an adequate fit to data in cases where the logistic curve is clearly inappropriate.

Selectivity data are count data, and in fitting selection curves to these data it is usual to assume that the counts are binomially distributed (McCullagh and Nelder 1989). Within a single selectivity haul, the binomial assumption is appropriate if the fish encountering the gear behave independently. It is common practice to fit a selection curve to the data combined over all successful hauls, and for the binomial assumption to remain valid it is then also necessary to assume that selectivity does not vary between hauls. This assumption is not valid in general, owing in part to variables such as catch size and haul duration. Gear saturation may occur for high catch sizes because of reduced selectivity in the latter part of the tow caused by meshes becoming clogged with fish (e.g., Suuronen and Millar, 1992) or distorted by the strain upon the gear. Hauls of longer duration may increase selectivity (e.g., Clark 1957) by allowing fish more time to escape, notwithstanding that the effect will be confounded with catch size.

If between-haul variation is not of primary interest, then fitting a selection curve to the combined hauls data remains a reasonable approach because the estimated selection curve parameters are quite insensitive to violation of the binomial assumption (McCullagh and Nelder, 1989). The combined hauls approach can be viewed as modelling the "average" $r(l)$, where the average is over the population of all hauls that could be made on that fishery. The selectivity hauls must therefore be a representative sample from this hypothetical population.

Between-haul variation does, however, invalidate the estimates of variability for the parameters of the combined hauls fit. To correct for this it is common to apply a goodness-of-fit based correction to the estimated standard errors (McCullagh and Nelder, 1989), but Fryer (1991) has demonstrated that this can underestimate the effect of between-haul variation. Suuronen and Millar (1992) corrected the standard errors by using the replication estimator of dispersion (McCullagh and Nelder, 1989, p. 127). This is a nonparametric estimator that is analogous to the pure error sums of squares estimator of linear regression analysis (Myers, 1990). The replication estimate of dispersion has an approximate chi-squared distribution when there is no between-haul variation and within-haul

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variation is binomial. When between-haul variation is present the approximate chi-square distribution no longer holds because the replicates across different size classes are then not independent. Nonetheless, the estimator provides a correction to the standard errors that incorporates both between-haul variation and within-haul variation.

If between-haul variation is of specific interest then fits to individual haul data are required. Fryer (1991) and Reeves et al. (1992) modelled between-haul variability by permitting parameters a and b of the logistic curve (1) to vary between hauls according to a bivariate normal distribution which can be estimated from the individual haul fits. Suuronen et al. (1991) and Suuronen and Millar (1992) regressed the estimated l_{50}'s for individual hauls against their catch sizes, and in four of five separate selectivity trials a decrease in l_{50} with catch size was indicated, though only one of these was statistically significant at the 5% level. These regressions used weights given by the inverse of the estimated variance of the individual haul l_{50}'s.

In the next section it is shown that neither the individual haul or combined hauls data from a scallop dredge selectivity study could be adequately modelled by any of the above mentioned approaches and that extreme between haul variation was present. A nonparametric analysis of the combined hauls data was implemented and between-haul variability was incorporated into the estimates of reliability through bootstrapping. The approach assumed

A1) the selection curve $r(l)$ is a nondecreasing function of l.

In addition, being a combined hauls approach, it was also assumed that

A2) the selectivity tows were representative of tows on the fishery.

Material and methods

Selectivity trials

Selectivity trials were performed onboard the 82-m stern trawler *Gadus Atlantica* during the last week of August 1991 as part of an Iceland scallop (*Chlamys islandica*) biomass survey for the St Pierre Bank (off the South coast of Newfoundland). The objectives of the study were 1) to summarize the retention properties of the survey dredge by estimating the shell heights l_{25}, l_{50} and l_{75} corresponding to 25%, 50% and 75% retention, and 2) to estimate the survey dredge's percent retention (by meat weight) of commercial sized (≥60 mm shell height) scallops.

The survey dredge was a 3.66-m (12-ft) wide offshore scallop dredge with belly constructed from 3 inch (inside-diameter) metal rings joined together with metal links. One selectivity tow was performed at each of ten locations randomly chosen within the survey area. For these tows, shrimp netting covers (35 mm inside mesh opening) were attached behind the dredge, and chafing gear was used under the bottom cover. The covered dredge was towed over the distance (1.0 nautical mile) and at the speed (3.0 kn) used in regular biomass survey tows. The contents of the dredge and covers were separately dumped, carefully picked over, and all Iceland scallops were removed. The scallop catch was weighed and a representative sample of between 20 and 40 kg (200–400 scallops), or the entire scallop catch if less than 20 kg, was taken for measurement. Each scallop in the sample was measured to the nearest millimetre in shell height. The catch weights were then used to estimate the size frequencies for the entire catch in the dredge and covers.

Selectivity analysis

We had planned to perform parametric analyses of the individual haul and combined hauls data using the standard maximum likelihood (McCullagh and Nelder, 1989) theory of the binomial model to choose the most appropriate form of the selection curve from those discussed above. However, as seen in the Results section, neither the individual haul nor combined haul data were amenable to parametric analysis.

Although it may not be possible to specify a parsimonious parametric form for the selection curves, it is at least reasonable to insist that they be nondecreasing. That is, the larger a scallop, the greater its chances of being retained in the dredge. The nonparametric statistical technique of isotonic regression fits nondecreasing curves to data. When the data are binomially distributed then the isotonic regression curve is the maximum likelihood fit to the data (Barlow et al., 1972, p. 38).

Isotonic regression curves are piecewise linear and can be fitted in an intuitive way using the PAV (pool adjacent violators) algorithm (Barlow et al. 1972, p. 13). In this application, the essence of the PAV algorithm is to pool adjacent size classes whenever their observed retention proportions violate the nondecreasing constraint. Isotonic regression views this violation as an artifact due to insufficient numbers in the "offending" size classes and so the pooling results in a block of size classes having a common observed retention proportion.

Barlow et al. (1972) show that the isotonic regression curve is unique and does not depend on the order

in which violators are pooled. The PAV algorithm can be implemented on computer as follows: Initially, treat all size classes as blocks of size 1. At each step of the algorithm there is an active block which is compared with the adjacent block in the active direction. The latter will be denoted L or R for active directions left and right, respectively. The initial active block and active direction are the smallest size class and R, respectively. The smallest size class is deemed to satisfy the nondecreasing constraint in active direction L. The PAV algorithm proceeds as follows:

B1) If comparison in the active direction results in violation of the nondecreasing constraint, then the two blocks are pooled to form a larger active block and the active direction becomes (or remains) L.

B2) If comparison in the active direction does not violate the nondecreasing constraint then the active direction becomes (or remains) R. In addition,

- if the active direction was L then the active block remains the active block.
- if the active direction was R then the active block becomes the next block on the right.

After a finite number of steps, the algorithm terminates when the rightmost block is active and R is the active direction.

If the observed retention proportions are nondecreasing for increasing l, then the isotonic regression curve is simply given by connecting all the proportions together with straight line segments. If the isotonic regression curve fitted to the observed retention proportions is flat (corresponding to a pooled block) at 0.25, 0.50 or 0.75, then the estimated l_{25}, l_{50}, or l_{75} is given by the shell size that is the midpoint of that pooled block.

For this study, published FORTRAN code (Cran, 1980) for implementation of the PAV algorithm (Barlow et al., 1972) was interfaced to the *Splus* statistical package.

Isotonic regression does not provide an estimate of the standard errors of the estimated l_{25}, l_{50}, and l_{75}. These were obtained by bootstrapping the data (Efron, 1982). To this end, the individual selectivity hauls were used to define a "population" of hauls. To include between-haul variability, the bootstrap resamples (with replacement) from this population. Within each resampled haul the retention proportions were also bootstrapped to include within-haul variability. That is, for each size class, the bootstrapped retention proportion was the proportion of dredge caught scallops in a sample taken with replacement from the captured (in dredge and covers) scallops of that size. The bootstrap samples were the same size as those represented in the data. For example, in haul 1 there were 48 scallops of 70-mm shell height, of which 28 were caught in the dredge. For this size class, a bootstrap sample of 48 scallops was taken by sampling with replacement from the 48 scallops whenever haul 1 was selected for the bootstrapped combined hauls.

The above resampling scheme was performed 200 times and on each occasion l_{25}, l_{50}, and l_{75} were estimated from isotonic regression fits to the combined hauls data, and percent retention (by meat weight) of commercial sized scallops was calculated by using the shell height to meat weight relationship given in Naidu (1991).

Results

The first four tows were taken over a relatively smooth bottom consisting mainly of small stones and pebbles. The remaining six tows were taken over a rougher bottom consisting of larger stones, rocks and boulders. The data from tow 5 were discarded owing to a torn cover. The proportion of commercial-sized scallops was lower in hauls 1–4 (58%) than in hauls 6–10 (81%). The weight of trash (rocks, sea cucumbers, starfish, etc.) exceeded the weight of scallops in every haul, particularly so in hauls 6–10. A complete summary of the hauls can be found in Millar and Naidu (1991).

The replication estimate of dispersion, calculated over size classes with a total combined catch of at least 10 scallops, was 828 on 480 degrees of freedom. Under the null hypothesis, H_0: {No between-haul variation and binomial within-haul variation} the estimator has an approximate chi-square distribution, hence H_0 is rejected with P-value $<10^{-6}$. Binomial variation within hauls should be a reasonable assumption for scallops, so rejection of H_0 suggests significant between-haul variation.

Results of parametric analysis

Figure 1 shows, for each successful haul and combined-over hauls, the proportions of the covered dredge's catch of scallops that were in the dredge. These retention proportions can be extremely variable, especially for the smaller scallops, because of the low numbers encountered. Logistic curves fitted to these retention proportions are shown as dashed lines. The residual plots show that the fitted logistic curves are inadequate. This is particularly true for the combined hauls data. (The residuals plotted in Fig. 1 are deviance residuals, as defined by McCullagh and Nelder [1989, p.39].)

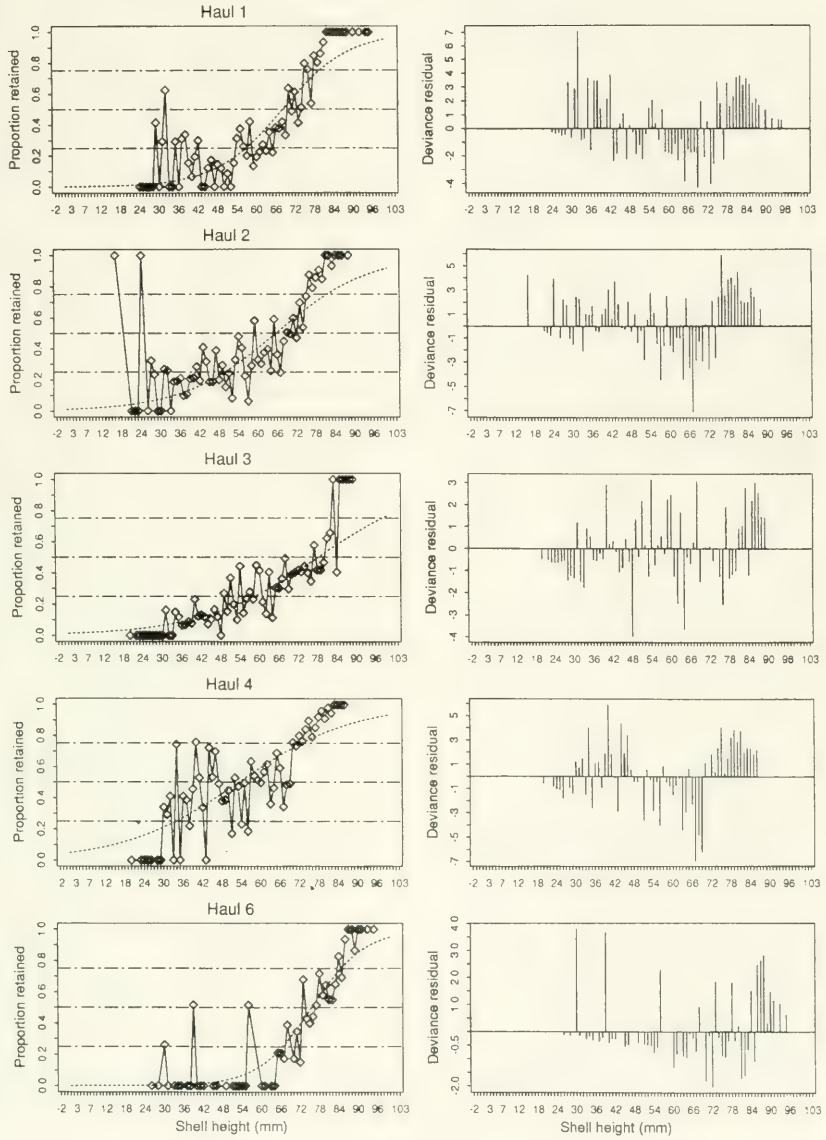

Figure 1

Logistic selection curves fitted to the individual haul and combined hauls data, and the deviance residuals from the fits.

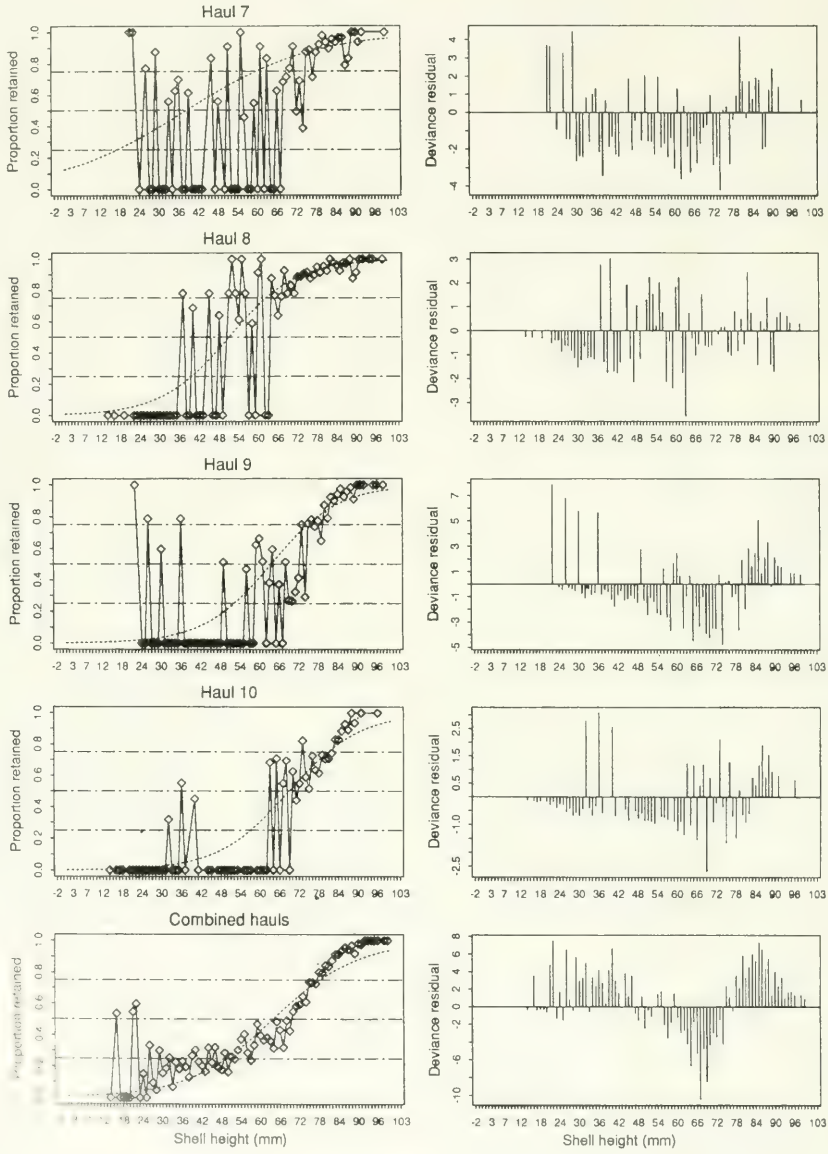

Figure 1 (Continued)

Logistic selection curves fitted to the individual haul and combined hauls data, and the deviance residuals from the fits.

Fits of the complimentary log-log, log-log, and Richards curve were also used on the individual haul data. The complimentary log-log curve fits were marginally better than the logistic fits but were still clearly inadequate. The log-log curve fits displayed worse residual structure than the logistic fits. This is because the log-log curve has a longer tail to the right of l_{50}, whereas the data suggest a longer tail to the left. The three parameter Richards curve fits provided a big improvement and, though very hard to judge, fits to about half of the individual hauls appeared to be adequate.

Figure 2 shows the combined hauls data fits of the logistic, complimentary log-log, log-log, and Richards curves. The Richards curve fit is the only one that could possibly be considered adequate, though there is an obvious clustering of negative residuals for shell heights between 61 mm and 71 mm. Since this group of residuals contains the estimated value of l_{50} (66.8 mm) it is of some concern, and the fit was deemed to be inadequate. (One might consider performing a run's test (say) for independence of the residuals. However, the run's test would be very approximate since it assumes that residuals will be positive or negative with equal probability 0.5. This is not the case for these data, especially for the very small and very large size classes, even when the model is correct.)

Nonparametric analysis

The nonparametric selection curve fits to the individual haul and combined hauls data are overlaid on proportion-retained plots in Figure 3 and the corresponding estimated sizes of 25%, 50%, and 75% retention are given in Table 1. Note that the flat portions of the curves (Fig. 3) correspond to size classes that were pooled. Considerable variability in the estimated l_{50}'s is evident, the smallest being 45.3 mm (haul 7) and the largest 80.1 mm (haul 3). Figure 3 suggests that the estimated l_{50} for haul 7 may be very unreliable—there were relatively few scallops less than 70 mm in this haul and the observed retention proportions of the smaller scallops are extremely variable because of the low numbers caught.

The estimates of l_{25}, l_{50}, and l_{75} from the combined hauls fit were 50.5, 69.4, and 77.3 mm, respectively. The percentile method (Efron 1982, p. 78), was used to determine approximate confidence intervals from the bootstrap. This gave 95% confidence intervals for l_{25}, l_{50}, and l_{75} of 21.0–53.8 mm, 66.1–72.5 mm and 73.6–80.5 mm, respectively. The extremely large confidence interval on l_{25} reflects the paucity of data for the smaller scallops. Retention by meat weight of commercial sized scallops was estimated to be 73% with a 95% confidence interval of 63%–82%.

Discussion

Bootstrapping (resampling) the experimental units (selectivity tows) is a natural way to emulate the effect of between-haul variability. In doing so, one requires an automated procedure for fitting a selectivity curve to the bootstrapped combined hauls data. Isotonic regression is well suited to this task because the selection curve for the bootstrapped combined hauls will always satisfy assumption A1. In contrast, parametric selection curves may not be sufficiently flexible to adequately fit all the possible bootstrapped combined hauls data sets.

One Referee of this paper made the interesting suggestion that it may not matter that parametric fits to the combined hauls data or bootstrapped combined hauls could be inadequate, because the bootstrap procedure should nonetheless be applicable and any problems with the fits would be indicated by wide confidence intervals or indications of bias (e.g., Efron, 1982, p.33). To investigate this, Richards curves were fitted to the same bootstrapped combined hauls used in the nonparametric analysis. The combined hauls fit had l_{25}, l_{50}, and l_{75} of 48.5 mm, 66.8 mm, and 77.6 mm, respectively, and the 95% confidence intervals obtained from the bootstrap were 33.3–56.6 mm, 59.4–71.5 mm and 74.1–80.3 mm, respectively. These confidence intervals have widths of 23.3, 12.1, and 6.2 mm, respectively, compared with 32.8, 6.4, and 6.9 mm from the nonparametric fits. The percent retention value and its confidence interval were the same as for the nonparametric analysis. However, the more subtle and possibly more relevant consequence of bootstrapping with a parametric curve is that the bootstrap indicates the ability of the combined hauls parametric fit as an estimator of the parametric fit to the entire hypothetical population of tows on the fishery. The latter may not be adequately modelled by a parametric curve—but the bootstrap will not consider this. The isotonic curve can not suffer this deficiency since the selection curve for the entire hypothetical fishery will be nondecreasing.

It was assumed that the selectivity tows were representative of survey tows on the scallop fishery (assumption A2). The selectivity gear used here was a covered survey dredge and it was deployed under survey conditions on a random subsample of survey locations. Assumption A2 will therefore by reasonable provided that the covers on the dredge did not have significant impact on its selectivity. To address this question Millar and Naidu (1991) compared the catch in the covered dredge with that in an uncovered dredge that was towed simultaneously. There was evidence to suggest a possible cover effect for scallops below about 58-mm shell height. This is unlikely to affect the

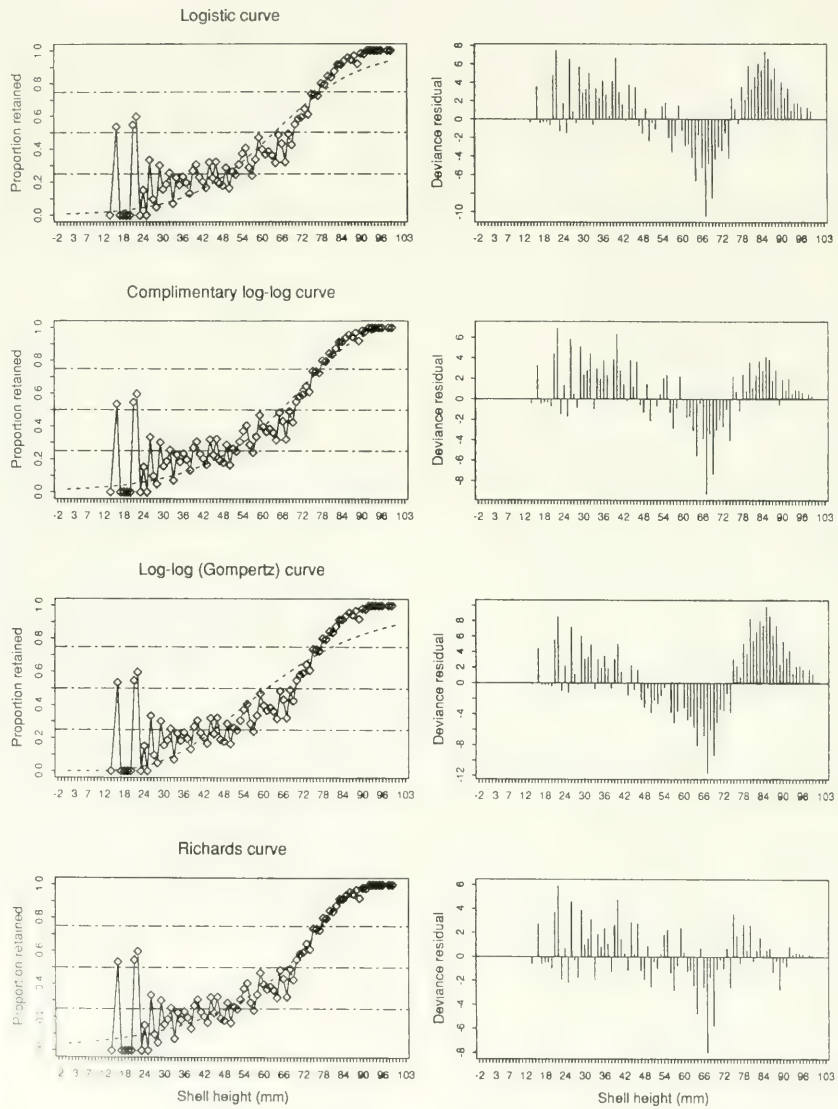

Figure 2

Logistic, log-log, complimentary log-log, and Richards curves fitted to the combined hauls data.

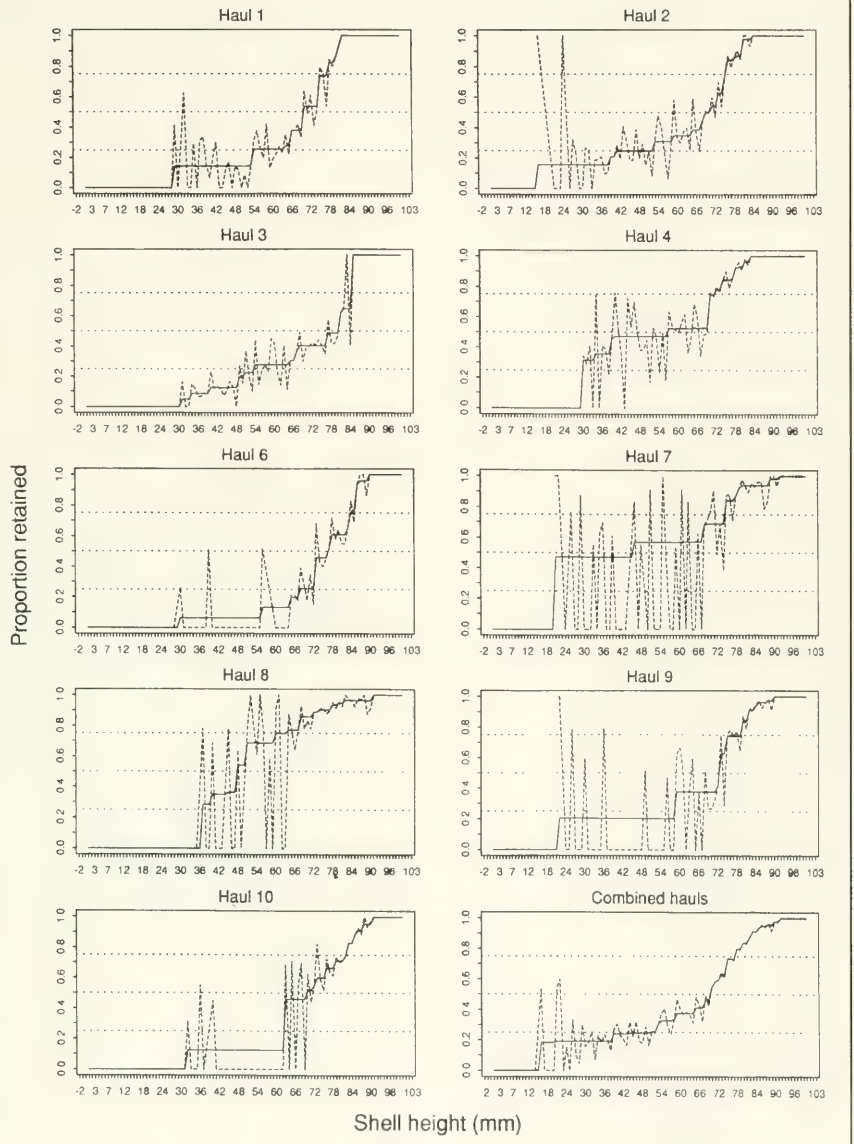

Figure 3
Isotonic selection curves (solid lines) fitted to the individual haul and combined hauls data (dashed lines).

Table 1
The estimated shell heights of 25%, 50%, and 75% retention for hauls 1–4, 6–10, and the combined hauls data, obtained by isotonic regression.

Haul	l_{25}	l_{50}	l_{75}
1	54.0	69.8	77.1
2	52.0	70.0	75.1
3	53.5	80.1	84.3
4	29.8	56.5	71.2
6	67.9	76.7	83.9
7	20.5	45.3	74.4
8	36.9	47.8	63.1
9	58.3	72.4	79.1
10	62.4	69.7	82.1
Combined	50.5	69.4	77.3

isotonic fit estimates of l_{50}, l_{75} or percent meat weight retention because bad data for small sizes will not affect the fit to large sizes. The same may not be true of parametric fits.

Acknowledgements

This work would not have been possible without the logistical support provided by K.S. Naidu and the programing assistance of Noel Cadigan, both of the Department of Fisheries and Oceans, St. John's, Newfoundland, Canada.

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Biological observations from the Cobb Seamount rockfish fishery

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The Cobb Seamount was discovered in 1950 by the crew of the fishery research vessel *John N. Cobb* (Anonymous, 1950). This submerged volcanic mountain (Budinger, 1967) is located approximately 280 nautical miles (nmi) off the southern Washington coast and comes to within 50 meters of the sea surface. At the 200-m isobath, its area is approximately 32 nmi^2 (Budinger, 1967). Various efforts have been made to study the biological, oceanographic, and geologic characteristics of the seamount since its discovery (Budinger, 1967; Birkland, 1971; Dower et al., 1992), but these efforts have been somewhat limited in scope and duration. The studies have shown that the seamount has concentrations of commercially valuable species including rockfishes (genus *Sebastes*). Most of the information about commercial fishing operations on the seamount is anecdotal and speculative, primarily because the seamount is located outside the Exclusive Economic Zone (EEZ) and therefore fishing vessels operating there are not subject to fishing regulations or routine sampling. What is known, however, is that bottom trawl, midwater trawl, gill net, and longline fishing has occurred at various times.

Foreign and domestic fleets have fished on the Cobb Seamount from at least the mid 1960's (Sasaki, 1986). Most of the fishing operations appear to have been aimed at several species of rockfish. Sasaki (1986) suggests that prior to 1985, there was intense fishing pressure on the seamount by the Japanese fishing fleet. In 1985, a few fishermen from Oregon attempted to trawl on the Cobb Seamount but were unsuccessful. It is not known why these efforts failed. Little fishing activity is believed to have occurred on Cobb Seamount between 1985 and September 1991.

In 1991, fishermen from Oregon and Washington returned to Cobb Seamount; this time they were successful. This success drew the attention of fishery managers because fish caught outside the EEZ are not regulated by the west coast Fisheries Management Plan governing nearshore stocks. Because of the regulatory problems presented by this new fishery, port samplers were instructed to give a high priority to sampling of landings from Cobb Seamount in part as an effort to identify any unusual characteristics which might make landings identifiable. In this paper we present some of the unique characteristics of the fish populations found on Cobb Seamount, particularly widow rockfish (*S. entomelas*). This seamount is isolated enough from coastal fish populations so that recruitment dynamics, density dependent growth, and bioenergetic studies could provide valuable new insights into fisheries biology.

Methods

Landings of commercially important groundfish are routinely sampled by biological technicians in Oregon according to standard protocols. Landings of fish from Cobb Seamount were sampled by port samplers in Oregon at two or three times the normal level and the majority of landings were sampled. All samples of widow rockfish were taken from vessels by using midwater trawl gear with the same mesh size as used in the nearshore widow rockfish fishery. During a four-month period, 11 landings were sampled by taking multiple 50-pound subsamples from each landing. Fork lengths were obtained from 891 widow rockfish, otoliths were removed from 724 of these fish for age determination by the broken and burnt method (Chilton and Beamish, 1982).

Mean length-at-age, age composition, and physical characteristics of the otoliths were compared to samples collected from landings of widow rockfish caught in the nearshore areas of the northern Oregon-southern Washington coast. To eliminate yearly and seasonal bias, comparisons of nearshore widow rockfish to Cobb Seamount widow rockfish were limited to the same months and years for both groups. To compare mean length-at-age of Cobb widow rockfish to the nearshore widow rockfish, only six-year-old fish could be used because of the small number of fish in other

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age groups for both areas. Otoliths were visually inspected without a microscope to look for gross morphological differences.

Results and discussion

Several unique features were observed in the landings of widow rockfish from Cobb Seamount. Mean length-at-age was similar for six-year-old widow rockfish in both areas; however, size composition, age composition, and physical structure of the otoliths were very different between the two areas.

Mean length of six-year-old widow rockfish on the Cobb Seamount was 35.3 cm FL (n=72, SE=0.11) and 37.3 cm FL (n=140, SE=0.09) for males and females, respectively. In the nearshore samples, the mean length of six-year-old fish was 35.3 cm FL (n=53, SE=0.22) and 37.8 cm FL (n=52, SE=0.26) for males and females, respectively. This suggests that mean length-at-age, at least for young fish, is similar between fish caught on the Cobb Seamount and fish caught in the nearshore area. Assuming that the fish on the seamount spent the majority of their lives there, then it is reasonable to assume that conditions affecting growth (temperature, food availability, competition, etc.) are probably comparable to the conditions found in the nearshore environment.

In the northern Oregon-southern Washington area of the Pacific coast, the mean length of widow rockfish in the commercial landings is 38.4 cm (Pearson and Hightower, 1991). In contrast, the mean length of widow rockfish from Cobb Seamount was 33.1 cm. Age composition of the widow rockfish in the landings from the Cobb Seamount is also very different from those in the landings from the nearshore area (Fig. 1). Only 7.5% of all fish collected from the Cobb Seamount were more than six years old, while 85.7% of fish collected from the nearshore samples were more than six years old (Fig. 1). This difference in age composition cannot be explained by differences in gear type because the same gear and mesh size was used in both areas. There are several potential explanations for these differences including differences in fishing pressure, differences in fishing behavior, differences in discard practices, and actual differences in the population age composition.

The argument for differences in fishing pressure relies on the belief that widow rockfish on the Cobb Seamount were heavily exploited prior to 1985 and therefore their population was reduced to very low levels. This argument is supported by Sasaki (1986) who reported that the seamount had, in fact, been heavily fished. Widow rockfish were never specifically mentioned as having been caught by any fishery prior to 1991. While intense fishing pressure on the Cobb Seamount may be responsible for the absence of older widow rockfish, there are arguments against this explanation. First, a sample of 50 harlequin rockfish (*S. variegatus*) had a mean age of 15 years, much older than would be expected if they had experienced similar fishing mortality to the widow rockfish. In addition, even if the Cobb Seamount had experienced extremely heavy fishing pressure, it seems unlikely that virtually all the older fish would have been caught.

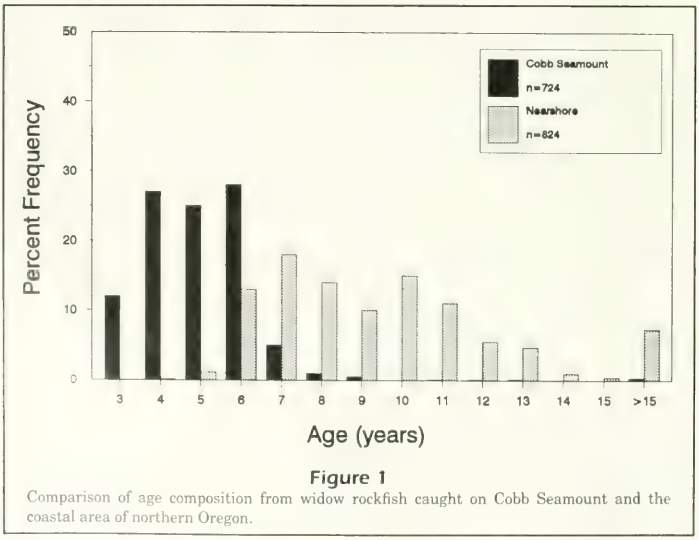

Figure 1
Comparison of age composition from widow rockfish caught on Cobb Seamount and the coastal area of northern Oregon.

The argument for differences in fishing behavior has some merit. Fishermen report that the terrain on the Cobb Seamount is very rugged and it is possible that the fishermen tend to keep their nets higher off the bottom to avoid snags than they would in the nearshore areas. This could result in a different age composition if young fish tended to disperse higher into the water column than older fish.

The argument for the difference in age composition being due to a difference in discard practices also has some merit. Fishermen operating under trip limits in the nearshore areas, and having to deal with market demands for larger fish, would tend to discard smaller fish. The problem with this argument is that it would tend to explain a higher proportion of small fish in the Cobb Seamount widow rockfish landings, but it would not explain the virtual absence of older, larger fish which certainly would be retained by the fishermen.

The possibility that the age composition of the two areas is actually different also has merit. It is not known whether the population of widow rockfish on the Cobb Seamount is self sustaining or if the fish recruit to the seamount from the nearshore population. Juvenile rockfish have an extended pelagic phase. During this stage they can be advected offshore. Recent studies of juvenile rockfish off the central California coast have found juvenile rockfish more than 200 miles offshore[1]. If this also occurs off Oregon, then it is possible that some fraction of the existing population on the Cobb Seamount originated as juveniles or larvae, or both, in the nearshore area. While it cannot be completely discounted that adults migrate to the seamount it seems unlikely because adult widow rockfish are not considered pelagic and the seamount is more than 200 miles from the nearest suitable habitat. It is possible that older fish either emigrate from the seamount or experience high mortality for some unknown reason. It is also possible that there was a massive kill of widow rockfish on the Cobb Seamount prior to 1985. Another possibility is that there never were widow rockfish on the Cobb Seamount prior to 1985. This latter possibility may have some merit since yellowtail rockfish appear to be totally absent from the Cobb Seamount; yet, they are quite abundant in the nearshore area, although the habitat at the Cobb Seamount would seem to be ideal for them. If getting to the Cobb Seamount is a fortuitous event, then it is possible that yellowtail rockfish just have not been lucky yet and that widow rockfish have only been lucky recently. Only further studies can determine the cause for the apparent differences in age composition between the Cobb Seamount and the nearshore populations.

Otoliths from many species can undergo a process of vaterite replacement (Gauldie, 1986) in which the aragonite in the otoliths is replaced by vaterite. This process results in a quite distinctive otolith morphology (Fig. 2) and has been observed by the authors in many species of rockfish, flatfish, and other groundfish species. Vateritic otoliths are sometimes called "resorbed" or "crystallized" owing to their somewhat crystalline appearance. In nearshore widow rockfish sampled in Oregon from 1991, only 2.5% of the fish had vateritic otoliths. In contrast, 28 percent of otoliths from Cobb Seamount widow rockfish are vateritic. Gauldie (1986), working with salmon, suggested that vaterite replacement is under single locus genetic control but can be overridden by temperature extremes. It is possible that Cobb Seamount could be subject to temperature extremes during certain oceanographic events like El Niños.

Three other interesting observations have been made about rockfish from Cobb Seamount during this fishery. Rosy rockfish (*S. rosaceous*) was caught; thus a northern range extension for this species was created.[2] Harlequin rockfish have been caught; thus, their southern range has been extended from its previously reported southern limit of Queen Charlotte Sound, British Columbia (Eschmeyer et al., 1983). Five shortbelly rockfish (*S. jordani*) were caught, three of them in excess of 34-cm fork length, which exceeds the largest fish previously known to the authors (33 cm). Studies on other seamounts in the Pacific have shown that rare species, exceptionally large specimens, and range extensions occur on other seamounts (Hughes, 1981).

The Cobb Seamount undoubtedly holds many other surprises for fisheries biologists. Studies of rockfish communities on the Cobb Seamount and how colonization occurs could lead to a better understanding of the population dynamics of this large, valuable group of groundfish. One possible way colonization could occur would be if it were found that strong cohorts on the Cobb Seamount were weak cohorts in the nearshore area and vice versa. This would suggest the possibility that advection of juveniles has an important role in determination of cohort strength which would have major ramifications in management of nearshore fisheries. Continued examination of fish with vateritic otoliths could yield new information, particularly if other populations of fish are found to have a high percentage of vateritic otoliths. Remotely operated vehicle studies would be a useful approach to examine the benthic community to determine its similarity to nearshore areas.

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Figure 2
Two sagittal otoliths from a widow rockfish. Otolith on the left is normal, while the otolith on the right exhibits the phenomenon known as vaterite replacement.

Effects of body size on probability of predation for juvenile summer and winter flounder based on laboratory experiments

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Predation by brown shrimp (*Crangon crangon*) has been hypothesized to impose significant mortality on settling juvenile plaice (*Pleuronectes platessa*) in European waters (Edwards and Steele, 1968; Lockwood, 1980; Veer and Bergman, 1987; Pihl, 1990). Laboratory experiments found that predation rate was dependent upon prey density and that predation, estimated by gut content analysis, could be the source of previously unexplained density-dependent mortality of early juvenile plaice in the Wadden Sea (Veer, 1986; Veer and Bergman, 1987). An important finding of this work is that predator and prey body size may have profound effects upon rate of predation and that recently settled plaice (under 30 mm) are much more vulnerable to predation than are larger fish. We were prompted to investigate the role of the sevenspine bay shrimp (*Crangon septemspinosa*) as a predator on metamorphosing and small juvenile summer (*Paralichthys dentatus*) and winter (*Pleuronectes americanus*) flounder because 1) all of these species are abundant components of New Jersey estuaries, 2) they all co-occur temporally, 3) the sevenspine bay shrimp is morphologically similar to the European brown shrimp, and 4) fish scales were present in the guts of this shrimp (Wilcox and Jeffries, 1974). We conducted laboratory experiments to determine the size range over which juveniles of these fish species may be susceptible to predation by sevenspine bay shrimp.

Methods

We used small cylindrical glass bowls, 197 mm diameter, containing 2 cm of washed sand (sufficient for both predators and prey to burrow in), filled with seawater to a depth of 50 mm. We conducted all experiments at prevailing ambient water temperatures (Table 1) by immersing the bowls in a flow-through seawater bath.

We collected transforming and juvenile winter flounder in May–July, 1990 and summer flounder in January–February 1990, with nightlights, plankton nets, and seines. Adult sevenspine bay shrimp were collected (January–July) by using a seine. All collections were made in the Great Bay-Little Egg Harbor estuarine system (New Jersey). In the laboratory, we fed experimental animals in excess (shrimp-chopped fish and shrimp; flounder-live brine shrimp nauplii), and then starved them for 24 hours before the start of each experiment. After anesthetization (25 $mg \cdot l^{-1}$ MS–222) we measured body sizes (Table 1) of flounder (in mm, standard length [SL]) and shrimp (in mm, total length [TL], from the tip of the antennal scale to the end of the uropod, Price, 1962).

At the start of each trial, we placed one flounder into each container and allowed it to acclimate for 24 hours. We then introduced one shrimp into each container at approximately 1500 hours. All containers were covered with perforated clear plastic sheets and were left undisturbed for 18 hours. We ran the experiments under a natural light cycle (11 hours dark, 13 hours light, lights out at 1800) using fluorescent lighting. Because sevenspine bay shrimp are unlikely to forage during the day (Haefner, 1979), we introduced the shrimp three hours before darkness in order to reduce the likelihood of predation immediately following their introduction. We recorded water temperature at the start and end of each trial. For each experiment, we set up several control containers (prey present, predator absent) and observed no flounder mortality in these controls (n=15 for summer flounder, n=12 for winter flounder). At the termination of each trial we scored predation as plus or minus based on the presence or absence of a live flounder.

We repeated trials for winter and summer flounder and varied shrimp and flounder size (Table 1). Because settlement in summer flounder occurs earlier than winter flounder, experiments involving summer flounder were conducted during late winter and winter flounder experiments were conducted in the spring, resulting in different ambient water temperatures (Table 1). In trials involving winter flounder, we

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Table 1

Sample sizes and body sizes of sevenspine bay shrimp and flounder prey for laboratory experiments. Sample size refers to the number of individual predator-prey trials. Pearson correlation coefficients (r) are given for correlations of predator size with prey size to indicate random allocation of predator and prey sizes.

Prey	Temperature (°C)	Sample size	Size range (C.V.) Predator (TL)	Prey (SL)	r	P
Pleuronectes americanus	18	60	51–59 mm (4.2%)	9–46 mm (37.4%)	0.15	0.24
Paralichthys dentatus	9–12	135	27–65 mm (17.5%)	11–16 mm (7.1%)	0.03	0.70

used large shrimp to minimize the predator size effect, thereby concentrating on prey size to determine if there was a size refuge for winter flounder. In trials involving summer flounder, we used a large range of predator sizes, but a narrow range of flounder sizes (those in the last stage of eye migration) because of the greater availability of the latter. This combination of predator and prey sizes was used to establish the relationship between shrimp size and their ability to successfully prey upon small summer flounder. In all trials, we randomly allocated predators and prey to the bowls to avoid deliberate or inadvertent size biases.

We used logistic regression analysis (SAS/STAT Users guide, Release 6.03 Edition 1988), which uses maximum likelihood analysis of the natural logarithm of the ratio of these response frequencies (logits) to estimate parameters of a linear model. Because the response is a frequency response rather than a continuous response, a chi-square value is calculated to test for the significance of the treatment variables. Once parameter estimates of the linear model have been made, expected logits can be generated. Expected probabilities of mortality can then be calculated using the following relationship:

$$m = \frac{e^L}{1+e^L}$$

where m is the probability of mortality from predation, e is the root of natural logarithm and L is the logit predicted by the linear model. This relationship is obtained by solving the following simultaneous equations for m:

$$m+s=1$$

and

$$\ln\left(\frac{m}{s}\right) = L$$

where s is the probability of survival.

Results

Sevenspine bay shrimp consumed both flounder species under laboratory conditions, and size effects were important in all interactions. In summer flounder trials, both prey and predator size significantly affected the outcome of prey-predator interactions (predator size χ^2=24.07, P<0.0001, prey size χ^2=7.75, P<0.01). Summer flounder matched with larger shrimp experienced generally greater mortality than those matched with smaller shrimp (Fig. 1A). Logistic regression of these data produced a positive relationship between probability of predation and shrimp size (Fig. 1B) which was stronger when the effect of flounder size was controlled using linear regression and the residuals were plotted against predator size (Fig 1C). Smaller summer flounder experienced higher mortality (Fig. 2A); however, probabilities from logistic regression show no clear pattern (Fig. 2B) because of the confounding effect of predator size. When we controlled the predator-size effect, a clear negative relationship was revealed between summer flounder size and probability of predation (Fig. 2C).

For winter flounder, the effect of flounder size on the probability of predation was significant (χ^2=4.03, P<0.05), but no significant predator size effect occurred (χ^2=0.04, P>0.8) presumably because we deliberately selected large shrimp in these trials in order to minimize this effect. Only the smallest individuals (<17 mm SL) were preyed upon (Fig. 3A). Logistic regression analysis demonstrated that the highest probability of predation was on the smallest individuals (>60% for 9 mm SL). This probability declined to zero at flounder lengths of approximately ≥17 mm SL (Fig. 3B). Parameter estimates of the prey size effect for both summer and winter flounder were similar (−0.4 ± 0.2 for winter and −0.6 ± 0.2 for summer), implying a similar size relationship for both species.

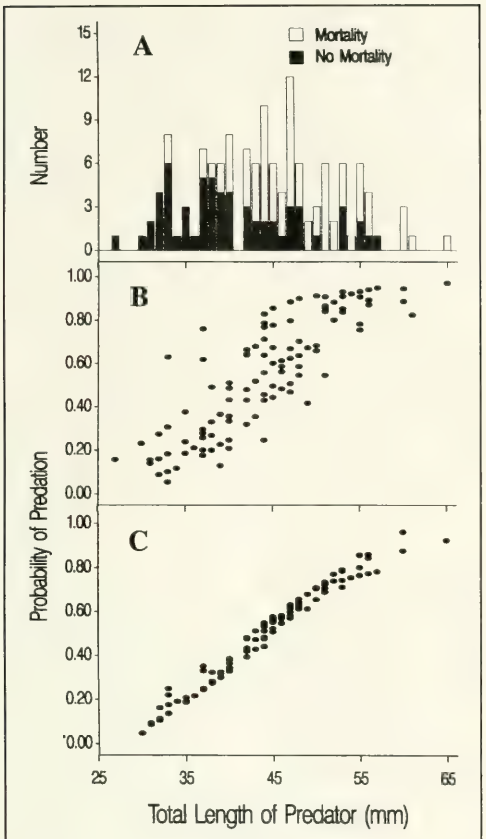

Figure 1

Relationship between size of sevenspine bay shrimp predators and predation on summer flounder prey. Graph presents original data with sample sizes above each bar (**A**), raw probabilities as predicted by logistic regression (**B**), and probabilities after being standardized for the effect of prey size (**C**). These probabilities and those for Figure 2 are based on the equation: Logit = 1.66+(0.15 * predator size)–(0.59 * prey size). See text for discussion of logits.

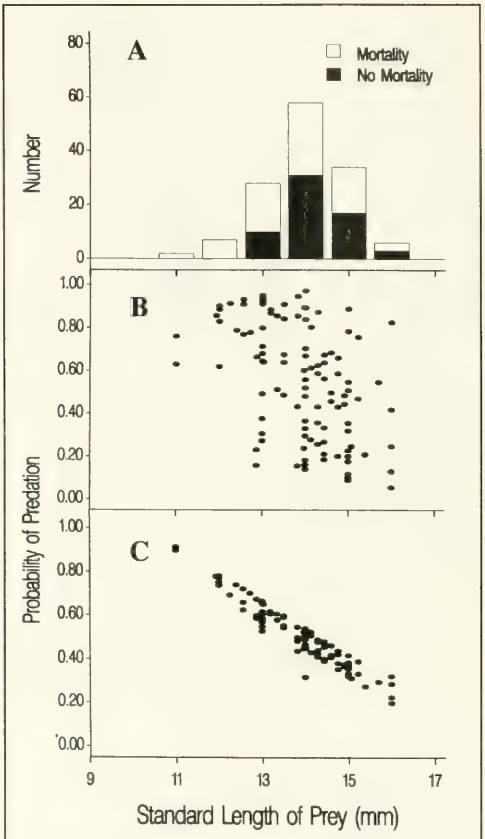

Figure 2

Relationship between prey size and probability of predation on summer flounder by sevenspine bay shrimp. Graph presents original data with sample sizes above each bar (**A**), raw probabilities as predicted by logistic regression (**B**), and probabilities after being standardized for the effect of predator size (**C**).

Discussion

Summer and winter flounder that survive the egg and larval stage and settle to estuarine substrates inhabited by adult sevenspine bay shrimp may be subject to significant predation. Summer flounder of 11–16 mm SL, the size at which they enter the estuary (Szedlmayer et al. 1992, Keefe and Able, 1993), are vulnerable to predation by a large size range of sevenspine bay shrimp. This interaction is likely because these species co-occur under natural conditions. Previous studies indicate that abundance of adult sevenspine bay shrimp, in estuaries to the south and north of the study area (Modlin 1980, Price 1962), begin to increase in the fall and continue to do so until they reach a peak in the spring. This temporal pattern overlaps completely with the period (October–May) that summer flounder enter the estuaries of New Jersey (Able et al. 1990, Szedlmayer et al. 1992). These shrimp range from 10–50 mm TL (Price, 1962). Our data sug-

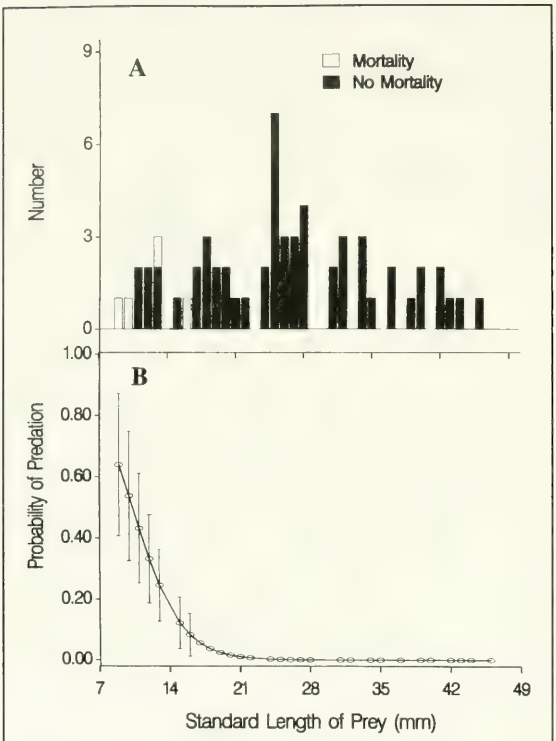

Figure 3

Relationship between size of winter flounder and predation by sevenspine bay shrimp. Figure presents original data with sample sizes above each bar (**A**) and predictions made by logistic regression (**B**). Bars on probabilities reflect one standard error of the estimate. These probabilities are based on the equation: Logit = 4.39–(0.42 * prey size).

gest that small summer flounder are vulnerable to predation over a large fraction of this range, with a 50% chance of mortality when encountering a shrimp of 45 mm TL (Fig. 1).

Winter flounder also settle (April–May) in northeastern U.S. estuaries (Pearcy, 1962) including those in New Jersey (pers. observ.) when adult sevenspine bay shrimp are abundant. Winter flounder settle at a smaller size than summer flounder (7.8 mm SL for winter flounder, Chambers and Leggett, 1987, vs. 13 mm SL for summer flounder, Keefe and Able, In press); however, our data indicate that the relationship between flounder size and vulnerability to predation is similar for the two species. This suggests that winter flounder must approximately double their size (i.e., reach approximately 17 mm) before they achieve a size refuge from predation by large sevenspine bay shrimp (Fig. 3). Both winter and summer flounder appear to exhibit a pronounced decrease in vulnerability to predation between 9 and 20 mm SL.

In summary, the vulnerabilities of both species of flounder were significantly affected by small differences in prey size. The duration of time spent within this size range (i.e., growth rate) can be quite variable depending upon habitat for winter flounder (Sogard, 1992) and temperature effects for summer flounder (Keefe and Able, 1993). Thus slight variation in size at settlement, or growth after settlement, may have important effects upon survival for both species. This scenario suggests that variability in stage duration, not rate of mortality, may be a critical determining factor of year-class strength as has been suggested by a number of authors (Sissenwine, 1984; Chambers and Leggett, 1987; Houde, 1987; Bailey and Houde, 1989).

Acknowledgments

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Movements of transplanted lingcod, *Ophiodon elongatus*, determined by ultrasonic telemetry

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Lingcod, *Ophiodon elongatus*, have formed an important component of commercial and recreational fisheries from Alaska to California. In the center of their range, however, in Puget Sound, Washington, and in the Strait of Georgia, British Columbia, Canada, lingcod stocks are currently depressed. For example, annual commercial catches in the Strait of Georgia declined from a high of 3300 metric tons (t) in 1944 to 80 t in 1989, probably owing to overfishing (Ketchen et al., 1983; Richards and Yamanaka, 1992). In 1990, the commercial fishery was closed; however, a restrictive recreational catch is still permitted. Similar declines in central Puget Sound led to a complete fishery closure between 1978 and 1982, followed by a small recreational fishery (Buckley et al., 1984).

Because of the value of the lingcod fishery, there is considerable interest in rebuilding these stocks. This paper describes a feasibility experiment for one approach to enhance natural stock rebuilding. Abundance is currently average or above average for lingcod stocks in offshore areas of the British Columbia coast (Richards and Yamanaka, 1992). Lingcod could be transplanted from these areas into the Strait of Georgia. Such an experiment was conducted by Buckley et al. (1984) in Puget Sound. They found that transplanted young-of-the-year lingcod (10–20 cm) were caught in the area 2 and 3 years after release. However, most transplanted adult lingcod left the area and migrated towards their capture site. Our experiment involved transplanting juvenile lingcod (age 2–3 yr) and tracking their movement in the new area through ultrasonic telemetry.

Ultrasonic telemetry has been used successfully on a number of marine fish species (Holland et al., 1985, 1990; Quinn et al., 1989; Clark and Green, 1990; Ruggerone et al., 1990; Matthews et al., 1990). Unlike conventional tags, ultrasonic tags allow continuous monitoring of fish movements. They are usually limited, however, to small sample sizes and short time periods because of cost and labour constraints. Ultrasonic telemetry was useful for this study because precise positions could be obtained for individual fish.

Matthews (1992) conducted a previous ultrasonic telemetry study on lingcod. In addition to tracking six stationary lingcod, she displaced five adult male lingcod a short distance (maximum 2.8 km) from their capture site. Four of these lingcod returned to their exact capture sites within 60 hours. Thus, she demonstrated that adult male lingcod were capable of homing over short distances. She concluded that transplants of adult male lingcod would likely be unsuccessful, given this tendency to home.

We addressed two issues left unanswered by Matthews (1992). In particular, we designed an experiment with juvenile rather than adult lingcod and we displaced these fish a relatively long distance (250 km). We determined whether lingcod remained at the transplant site over a period of approximately one month. Based on previous studies, we hypothesized that homing lingcod would leave the transplant area within a few days and exhibit directional movements towards the capture site. We compared the movements of transplanted lingcod with similar-size control lingcod caught, tagged, and released in the study area.

Methods

The experiment was conducted off the east coast of Vancouver Island, British Columbia (Fig. 1). The 12 × 4 km study area was chosen because it contained shallow reefs typical of lingcod habitat (Ketchen et al., 1983). The area was conveniently marked by navigational aids and separated from small islands to the north and east by a 300-m deep channel. A commercial fishery existed here historically, and recent SCUBA and recreational fishing activities confirmed the presence of a small resident lingcod population.

Experimental lingcod were collected at the end of September 1991 from Queen Charlotte Strait, about 250 km northwest of the study area (Fig. 1). They were held for 5–34 days before being tagged and released. Prior to tagging, lingcod were immobilized in an anaesthetic bath (MS222, tricaine methane sulphonate). Tags were then anchored through the dorsal musculature adjacent to the dorsal fin by means of two self-locking nylon ties (Holland et al., 1985). Tagged lingcod were held overnight to assess condition; only healthy-appearing

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Fishery Bulletin: 91:582–587 (1993).

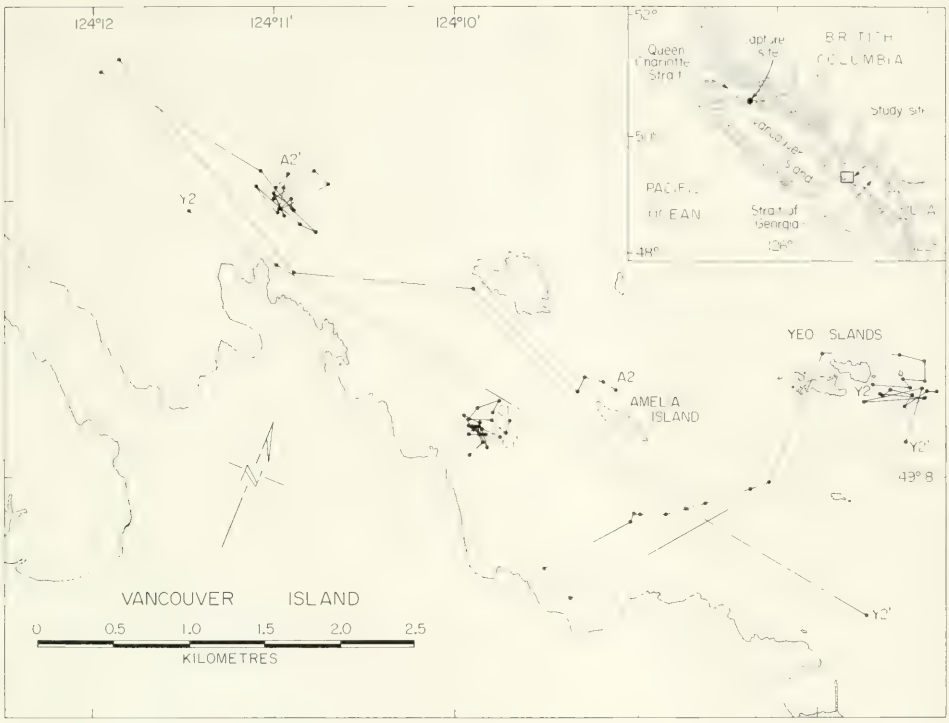

Figure 1

Location of the study area in the Strait of Georgia, British Columbia, and typical tracks of transient (fish Y2), resident (fish A2), and control (fish C1) groups of lingcod. The release site is indicated by the fish number and the prime symbol gives the last observed position. Fish Y2 left the study area, returned at position Y2', and was last observed at position Y2". A "." indicates each recorded position.

fish were used for the experiment. Experimental lingcod were released at one of two sites in the study area, either Amelia or Yeo Island (Fig. 1). Control lingcod were collected within the study area, held for 1–2 days, and released at their capture site.

Transmitters (Vemco Ltd., Armdale, Nova Scotia, Canada B3L 4J4) of two types were used, varying in battery life and size. A V3-5HI transmitter (16 × 95 mm) had one of four frequencies (60.00 Hz, 65.54 Hz, 69.00 Hz, 76.80 Hz) and six pulse rates. It weighed 34.5 g (in air) and had an expected battery life of 31 days. The smaller V2B-2L transmitter (8 × 38 mm) used identical frequencies but higher pulse rates. It weighed 11.5 g (in air) and had an expected battery life of 12 days. On average, fish weights were 40 times greater than the weight of the V3-5HI tag and 228 times greater than the weight of the V2B-2L tag (Table 1). Lingcod tagged with a V3-5HI transmitter could be detected at distances from 0 to 1 km, depending on the complexity of the habitat in which the fish was located. Detection range of the V2B-2L transmitter was approximately half that of the V3-5HI transmitter.

Two different strategies were used for tracking. A few fish were tracked continuously over a 2–3 day period; position of the fish was recorded at 1-hour intervals if the fish was stationary and at intervals as frequent as 10 minutes for rapidly moving fish. Other lingcod were located at least three times during a 12-hour tracking period and individually tracked for 30 minutes to 1 hour. We assumed that a lingcod left the study area if it could not be found after a search of the entire study area, provided that its transmitter was active (based on the manufacturer's estimate of battery life). We continued to search for each lingcod throughout the active life of its tag.

Table 1

Fish number, sex, fork length, weight, weight ratio of fish/tag (in air), release date, number of positions recorded, days between release and last recorded position, observed distance travelled, mean daily movement rate, and number (n) of 24-hour periods used to calculate mean daily movement rates for transient, resident, and control groups of ultrasonic-tagged lingcod.

Group	number	sex	length (cm)	weight (kg)	ratio fish/tag	release date	no. of positions	no. of days	distance (km)	movement rate km/d	n
Transient	A1	F	62	2.4	70	Oct 15	27	4	16.2	0.71	4
	A4	M	58	1.9	55	Oct 28	31	7	16.1	2.67	4
	[1]A5	M	53	1.4	275	Nov 4	7	2	3.2		
	Y1	M	54	1.5	44	Oct 7	68	4	12.5	1.79	4
	Y2	M	53	1.4	41	Oct 9	48	19	16.8	0.89	7
	Y6	M	51	1.4	41	Oct 23	15	7	9.2		
	Y7	F	52	1.3	38	Oct 28	11	2	5.1		
Resident	A2	M	52	1.3	38	Oct 18	41	24	8.1	0.61	6
	A3	F	48	1.1	32	Oct 23	24	28	6.0	0.74	7
	[1]A6	F	47	1.0	196	Nov 4	4	8	6.8		
	Y3	M	51	1.1	32	Oct 11	83	21	18.2	0.53	14
	Y4	F	46	0.7	20	Oct 14	64	21	17.4	0.56	12
	Y5	F	50	1.2	35	Oct 18	57	25	28.9	1.47	12
Control	C1	F	50	1.0	29	Oct 30	38	50	5.3	0.06	8
	[1]C2	M	49	1.1	216	Nov 1	19	27	0.7	0.06	7
	[1]C3	F	51	1.2	235	Nov 9	18	40	0.7	0.03	3
	[1]C4	M	49	1.1	216	Nov 9	16	34	0.6	0.03	3

[1] V2B–2L tag.

Results

Approximately 120 hours of daylight and 170 hours of nighttime lingcod tracking were conducted between 7 October and 23 December 1991 (Table 1). Seven experimental fish were released at Yeo Island (fish Y1-Y7) and six experimental fish at Amelia Island (fish A1–A6). There were an additional four control fish (fish C1–C4). Based on size, most tagged lingcod were estimated to be sexually immature and 2–3 years of age. Lingcod from this area mature over a size range of 50–62 cm for males and 60–67 cm for females (Richards et al., 1990). The largest male and female lingcod used in the study had lengths of 58 and 62 cm, respectively.

Seven of the 13 experimental lingcod left the study area at least 7 days prior to their transmitter expiry dates (Table 1). We termed these lingcod as "transients" and the remaining experimental lingcod as "residents." Resident and control lingcod could be detected in the study area until their transmitter expiry dates. With the exception of fish Y2, transient lingcod were last observed 2–7 days after release. By contrast, most resident lingcod could be located in the study area after 28 days. Control fish were recorded after even longer periods. For example, fish C1 (V3–5HI tag) was observed after 50 days. Similarly, fish C3 (V2B–2L tag) was observed after 40 days. All the control fish were located in shallow water (depth of approximately 20 m) and maintained relatively constant positions over the course of the study.

The amount of time spent in the holding tank did not appear to affect the tendency of experimental lingcod to leave or remain in the study area. Lingcod in transient and resident groups did not differ significantly in the number of days held before release (Wilcoxon rank sum test, $P>0.10$). However, fish length ($P<0.05$) and weight ($P<0.01$) did differ significantly between transient and resident groups of lingcod (Wilcoxon rank sum test). Although sample size was too small to consider sex or transmitter size effects, both sexes and transmitter sizes were represented in each experimental group.

In general, individual tracks were similar for lingcod in the transient group and in the resident group. For example, Fish Y2 (transient) was released at the south side of Yeo Island, moved counter clockwise around Yeo Island, travelled southwest to Vancouver Island, and then returned to the release site in 5 days (Fig. 1). Fish Y2 remained within 0.5 km of the release site over the next 2 days where it was observed by SCUBA divers. For the next 10 days, fish Y2 could not be detected in the study area. It was then found south of Yeo Island, moved 7 km west, and left the study area 19 days after release. Fish A2 (resident) was re-

leased at the north side of Amelia Island, moved in a westerly direction for 5 days, turned east, and then remained within a 0.3 km^2 area for 17 days, after which the tag battery expired. All four control fish remained within 0.4 km^2 of their capture-release site over the entire tracking period.

Transient lingcod were apparently more active than resident lingcod, and control lingcod moved little. An analysis of variance on the ranked movement rate data for the experimental lingcod indicated that rates differed significantly among fish within a group ($P<0.001$) and, furthermore, that rates differed significantly between fish in transient and resident groups ($P<0.001$). Similarly, movement rates differed significantly between experimental and control groups of lingcod ($P<0.001$). Mean (±SE) movement rates were 4.9±0.5 m/min, 1.8±0.2 m/min, and 0.3±0.2 m/min, respectively, for transient, resident, and control groups of lingcod. Movement rate was also related to fish size. For the experimental lingcod, rank correlation coefficients between mean movement rate and fish length (0.69) and weight (0.60) were significant ($P<0.05$). Thus, fish size may determine movement patterns, which in turn determine the tendency of experimental lingcod to leave or remain in the study area.

We calculated the total (horizontal) distance travelled by each lingcod (Table 1) as the sum of the distances between sequential observations of fish position. This measurement obviously depends on the number of positions recorded for a fish during each tracking period. Furthermore, the number of positions recorded was highly variable, because of continuous observations for some fish. We computed daily movement rates (km/d) to ensure meaningful comparisons among fish. These rates were calculated from distances between estimated positions at 24-hour intervals for fish with three or more sequential daily position observations. As demonstrated for the raw movement data, daily movement rates were significantly greater for transient fish than for resident fish (Wilcoxon rank sum test, $P<0.05$), and for resident fish than for control fish (Wilcoxon rank sum test, $P<0.001$). Mean (±SE) daily movement rates were 1.42±0.24 km/d ($n=19$), 0.80±0.13 km/d ($n=51$), and 0.05±0.01 km/d ($n=21$) for transient, resident, and control groups of lingcod, respectively.

Continuous observations for four experimental fish were sufficiently long to examine diel activity patterns. We determined the distance travelled between estimated positions at sequential 2-hour periods (Fig. 2). By late-October, the study area was experiencing only 8 hours of daylight. Lingcod travelled the greatest distances at night (Fig. 2). Movement rates for these fish averaged 2.1±0.3 m/min ($n=58$) during the night (1600–0800 hours) and 0.7±0.1 m/min ($n=26$) during the day (0800–1600 hours).

Discussion

Movements of lingcod transplanted 250 km from their normal habitat were related to fish size. The larger fish tended to disperse from the study site within a few days of release. These results corroborate the findings of Buckley et al. (1984); when lingcod are transplanted over large distances, the smaller fish are more likely to remain in the new area.

The tendency for larger experimental lingcod to leave the study area may be related to the onset of sexual maturity. Lingcod spawn in the Strait of Georgia between December and March (Low and Beamish, 1978). Lingcod selected for the transplant were all smaller than the size at 50% maturity. However, sexual maturity in lingcod can occur over a wide size range (Richards et al., 1990). For example, all experimental male lingcod and one transient female lingcod were larger than the size at 20% maturity. Thus, some of the recorded movements could be associated with selection of spawning (nest guarding) sites.

Ultrasonic tags provide short-term information on fish behaviour. Experimental lingcod could be followed for at most 28 days (Table 1) and we can not discount the possibility that resident lingcod left the study area after the end of the experiment. Furthermore, tran-

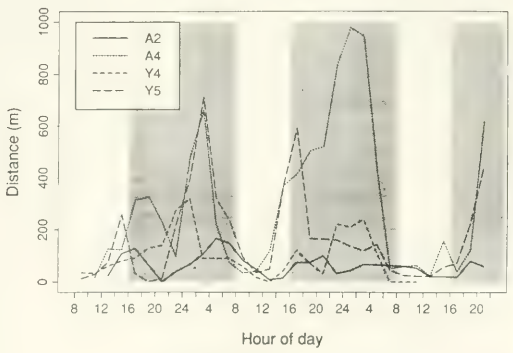

Figure 2

Distances travelled over 2-hour intervals by four lingcod observed continuously for 48–60 hours. Distances are shown corresponding to the interval midpoint. The shaded rectangles indicate periods of darkness.

sient lingcod may have become resident just outside the boundaries of the study area or returned at a later date. Fish Y2, for example, was apparently absent from the study area for 10 days before returning (Fig. 1). Conventional tagging studies are required to address these long-term issues. However, conventional tagging studies suffer from other problems. For example, the lack of fishing effort in the area due to seasonal closures would reduce the probability of tag recapture, and a minimum size limit (65 cm) would impose a size-selectivity on the recaptured fish.

Our measurements of lingcod movement rate were comparable to those reported by Matthews (1992). She observed movement rates of 1.17 km/d for displaced male lingcod, intermediate to the rates of 1.42 km/d and 0.80 km/d that we computed for lingcod in transient and resident groups, respectively. Furthermore, our estimate of nocturnal (1600–0800 h) movement rate was 2.1 m/min, identical to the rate that Matthews (1992) measured between 2400–0600 hours. The control lingcod in our study remained within the maximum home range size of 0.4 km^2 recorded by Matthews (1992).

It was not possible for us to determine whether lingcod moved toward their capture site after leaving the study area. Homing has been documented for adult lingcod (Hart, 1943; Cass et al., 1983; Matthews, 1992), but other factors undoubtedly affect fish movement. For example, the prevailing current in the Strait of Georgia flows to the northwest owing to land masses and prevailing winds from the southeast (Thomson, 1981). Hart (1943) observed from tag returns that most lingcod released in the Strait of Georgia moved in a northwesterly direction.

The purpose of this study was to determine whether stocking with juvenile lingcod could promote natural stock rebuilding. Because 6 of the 13 displaced fish did remain within the 12 × 4 km study area while their tags were active (28 days), restocking with juvenile lingcod is a potential enhancement tool. For transplanted fish to contribute to the spawning stock, they must remain in the new area and survive there until reproduction (spawning/nest guarding) is complete. Annual natural mortality rates for lingcod are 24% (Schnute et al., 1989). Mortality rates due to sport fishing and marine mammal predation may be higher (Collicutt and Shardlow, 1989; Olesiuk et al., 1990; Smith et al., 1990). To compensate for these mortalities, the number of age 2–3 year lingcod transplanted must be at least two to three times the number required to achieve a target spawning biomass one year later. A harvest of this magnitude could be detrimental to the donor stock. Until the depleated stock is re-established, the enhanced area should be closed to lingcod retention, and if possible, to all fishing activities. Hook and release mortality is not known but could decrease survivorship if fishing pressure is intense.

Acknowledgments

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Abstract.—Developmental Instability (DI) has been proposed as an inexpensive, quickly applied, and sensitive indicator of stress that can be utilized in early warning and in monitoring anthropogenic impacts on fish and other animals and plants. A problem arises, however, to the extent that natural stressors confound the effects of human-induced disturbances. Our objective in this work was to investigate whether a natural stressor, in the form of El Niño conditions, contributed to DI in the Pacific hake. Right-left (fluctuating) asymmetry of otolith length, width, growth rate, and weight, as well as right-left otolith shape differences, were used as measures of DI. Results show that indeed El Niño disrupts development, indicating stress. This outcome suggests that DI, as an early warning and monitoring tool for stress, must be used with caution.

Developmental instability as an indicator of environmental stress in the Pacific hake *(Merluccius productus)*

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The viability of fish populations and the ecological communities of which they form a part is a matter of concern to fisheries managers. At present, awareness of ecological problems often occurs only when stocks have already begun to decline, when there is clear evidence of disease or morbidity, or when die-offs occur.

Much work has been done on methods to assess adverse environmental impacts on fish via physiological stress measures (Adams, 1990a). These methods can, in theory, be used to monitor problems and, possibly, act as early warning indicators. However, most of these indicators either measure short-term acute stress response (e.g., corticosteroid levels), or are expensive and laboratory-intensive. They are cost-effective only in evaluating already obvious signs that a problem exists. In economically depressed areas, including the developing nations, these methods are impractical. In addition, they generally lack ecological relevance (Adams, 1990b).

A possible alternative to these methods lies in morphological measures of developmental instability by which changes (induced by environmental or genetical stress) in the basic developmental strategy of organisms can be assessed. For example, chronic stress might aggravate right-left asymmetry in normally bilaterally symmetric structures (Soule, 1967; Valentine and Soule, 1973; Valentine et al, 1973) or increase the number of aberrations in circulus patterns on scales (Shackell and Doyle, 1990). Morphological measures are inexpensive to obtain and cause minimal or no damage to animals involved. They can be quickly and inexpensively applied not only in situations where concern has already arisen, but also as standard monitoring tools. Screening of fry might be valuable in assessing effectiveness of various hatchery practices or in evaluating smolt quality in Pacific salmon.

The efficacy of right-left, or "fluctuating" asymmetry (FA) as an indicator of both genetic and environmental stress has been well documented. Within populations, homozygosity is associated with increased FA

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(Dobzhansky and Wallace, 1953; Lerner, 1954; Lewontin, 1956; Bader, 1965; Bruckner, 1976; Soule, 1979; Vrijenhoek and Lerman, 1982; Leary et al., 1983, 1984; Mitton and Grant, 1984). Increased homozygosity is one consequence of inbreeding (one form of genomic disruption). Within populations of outcrossing species, inbreeding is associated with lowered fitness (Lewontin, 1956; Charlesworth and Charlesworth, 1987). Bader (1965), Bailit et al. (1970), and Clarke (1992) have all found positive correlations among populations between inbreeding and FA.

The converse of inbreeding depression is outbreeding depression. Hybridization and subsequent introgression of sufficiently *different* populations can lead to the disruption of coadapted gene complexes and thus, in theory, promote both decreased fitness and developmental instability (Vrijenhoek and Lerman, 1982). Zakharov and Bakulina (1984) found that when individuals of similar populations of *Drosophila virilis* were crossed, no increases in FA over the parental types were observed. When more divergent strains were crossbred, FA was pronounced in the offspring. Outbreeding depression should be most apparent in interspecific hybrids. Leary et al. (1985) have found FA to be higher in laboratory hybrids of rainbow (*Oncorhynchus mykiss*) and cutthroat (*O. clarki*) trout than in either parental type.

Environmental disturbance, or deviation from the conditions to which organisms are adapted, leads to lowered fitness and developmental instability. Temperature stress causes increased FA in laboratory mice and rats (Beardmore, 1960; Siegel and Doyle, 1975, a and b; Siegel et al., 1977), in lizards (genus *Lacerta*, Zakharov 1982), and in chum salmon (*O. keta*, Beacham 1990). Audiogenic stress has the same effect on laboratory rats (Siegel and Smookler, 1973; Siegel and Doyle, 1975c). Valentine and Soule (1973) demonstrated that FA of laboratory grunion (*Leuresthes tenuis*) populations rose with concentrations of DDT. Clarke (1992) showed increased FA in pesticide-treated bush flies (*Musca vetustissima*) even at concentrations too low to produce statistically detectable changes in mortality. Zakharov and Rubin (1985) demonstrated the effects of contamination on FA in animals in the Baltic Sea. Thus FA may be an extremely sensitive indicator of stress.

Chronic stress indicators may be sensitive to naturally occurring events as well as anthropogenic disturbances. Zakharov et al. (1991), for example, found that intensified population density feedback led to increased FA during the decline phase of shrew population cycles. Data exist (Emlen, unpubl.) suggesting increased asymmetry occurs in the canine teeth of population-stressed northern fur seals. Clearly, if natural stressors are important contributors to developmental instability, then their effects must be considered when using DI as a tool for identifying or monitoring anthropogenic disturbances. In this paper we provide an example of FA responses to another natural stressor, the El Niño event of 1982–1983.

The Pacific hake (*Merluccius productus*) ranges along the Pacific coast of North America from Mexico to Alaska. Several genetic stocks can be distinguished. These include two spawning in Puget Sound, one from the Georges Straits, several from the fjords of Vancouver Island, and a so-called coastal population that ranges from San Francisco Bay to southern Baja California. Reproduction occurs from January to April, and young fish enter the fishery at about age three. Individual growth occurs largely between May and September.

Environmental conditions associated with the 1982–1983 El Niño may have caused significant dislocations of the coastal hake stock on the summer fishing grounds, since the entire population apparently moved northward (Francis and Hollowed, 1985). Length and weight information from the data set used by Francis and Hollowed and gathered by the National Marine Fisheries Service showed no significant differences between the 1980 and 1984 year classes for either sex. However, the 1980 El Niño year-class fish were slightly longer and lower in weight, and a Mann-Whitney test showed them to have significantly lower condition factor (weight/length^3) than the 1984 control year-class (respective means=0.06709, 0.07208; n=85, 63; P=0.0001). Both the dislocation in position and the diminished condition factor of population members suggest a drop in population viability and, thereby, implicate stress. Might this stress also have provoked developmental instability?

Methods

The development of otoliths, small calcareous structures used in maintaining balance in some fishes, is known to reflect growth rate and transition points in life histories (Wilson and Larkin, 1982; Volk et al., 1984; Alhossaini and Pitcher, 1988; Sogard, 1991). As such, they may be useful indicators of developmental instability. We do not suggest that otoliths fit the criteria given above for cost effectiveness and harmlessness to the organisms monitored. We use them here simply as a convenience (they were readily available and came with appropriate, attendant data on fish age, length, weight, and date of collection). The National Marine Fisheries Service, at its Alaska center in Seattle, maintains a collection of otoliths taken by scientific observers aboard commercial hake fishery boats. From this collection we obtained paired right and left

otoliths for 4-year-old hake caught in the first half of September for the years 1984 and 1988 (from the 1980 and 1984 year classes). These fish were the same from which the length and weight data, mentioned above, were taken. Individuals from the 1980 year class were in their second and third year of growth during El Niño; those from the 1984 year class were not present during the El Niño event. Time-sequential data is useful in the present context since the population was used as its own control, reducing or minimizing confounding factors of geography, genetic stock, etc.

Five otolith characters were used to assess instability: fluctuating asymmetry in weight, length, maximum width, growth rate, and right-left differences in shape (Fig. 1). For comparison of shape, one otolith was aligned with the reverse image of the other, and right-left shape differences examined. At least two means of alignment exist. Since otoliths show annual growth rings, it was possible to superimpose long axes drawn through the first growth ring. In the 1980 year class this ring was laid down just prior to the El Niño event and indicates the beginning of the period of stress. Measured differences along the outlines of the third ring, marking the end of El Niño, provide an appropriate measure of right-left differences in growth during the period. This approach was impractical.

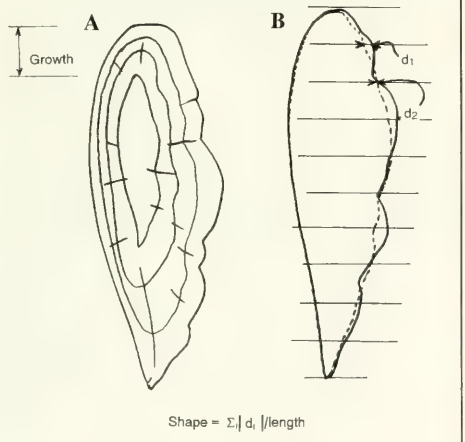

Figure 1

Hake *(Merluccius productus)* otoliths: **(A)** An otolith showing growth lines and the measure used to assess growth between ages 1 and 4; **(B)** Diagram of superimposed right and left otoliths showing how shape difference was characterized.

While distances between the rings could be reasonably approximated with the aid of an optical micrometer, our equipment was inadequate to permit video or photo reproduction of clear ring patterns. Accurate axes could not be drawn. Minute angular changes in axis definition generated large differences in the shape measure.

Because of these difficulties, we used an alternative approach. Equally magnified images of the two otoliths were projected onto paper and their outlines traced. One tracing was then turned over and placed atop the other. Each otolith possesses clearly marked "top" and "bottom" extreme points (Fig. 1), so alignment could be accomplished by superimposing the axes drawn through these two points. This procedure led to an almost perfect fit of the two otoliths along their straighter side and to clear pattern differences along their opposite scalloped side (Fig. 1). Nine equally spaced lines were drawn perpendicular to this axis, and, along each such line, the absolute distance between the scalloped margins of the two overlain outlines was measured. Right-left differences among the otoliths were taken as the sum of these absolute distances, normalized by dividing by the axis length. Information lost by neglecting similar differences along the straight side was negligible owing to the almost perfect fits along that margin. Growth rate was measured by the maximum distance, parallel to the straight side, between the first and the fourth otolith growth ring at the broader end of the otolith (Fig. 1).

Four-year-old fish caught in September, near the end of the growth season, may have displayed some variance in size owing to differences in date of hatching. This variance is not likely to be large because little growth occurs between earliest and latest hatching in January and April. Nevertheless, to correct for possible associations between asymmetry and early growth, we used a normalized index, $|L-R|/(L+R)$, with L and R designating left and right measures. Because collections for each of the three years were made at very nearly the same time, biases arising from possible influences of growth stage on asymmetry were minimized. The measure of right-left difference in shape is not a measure of FA in the strict sense (Palmer and Strobeck, 1986). However, an increase in the measure would indicate an increased deviation from normal developmental homeostasis. Thus it is a valid indicator of developmental instability.

Tests for fluctuating asymmetry depend on an absence of directional asymmetry (skew), anitsymmetry (bimodality or platykurtosis) and, according to one school of thought (Palmer and Strobeck, 1986), a normal distribution for $(L-R)/(L+R)$. The Shapiro-Wilk statistic (Zar, 1984, p. 95) was used to test for normality. Because of the controversy surrounding the validity of

FA tests for traits not normally distributed, further analyses were carried out twice, once with and once without such traits. A second order ANOVA was applied to test for influences of sex and year class on growth rate. Finally, fish were catergorized as fast or slow growers, according to whether growth rate fell above or below the median for the year in question, and a three-way MANOVA was performed to test for effects of growth rate, sex, and year on FA and right-left otolith shape differences.

Results

For both the 1980 and 1984 year classes, we found that the distributions of weight, width, and length did not differ significantly from normality (Table 1). These variables can, therefore, be used in analysis of FA. Growth rate was not normally distributed. The two-way ANOVA indicated no influence of sex (F=1.42; df=1, 141; P=0.234) and no significant interaction effect of sex X year (F=0.36; df=1,141; P=0.550) on growth. The main effect of year, however, was strong (F=14.20; df=1,141; P=0.0002). This last result, along with the possibility that growth rate might influence asymmetry of other characters, provided the rationale for incorporating growth rate into the three-way MANOVA, as noted above. Results were qualitatively the same—no differences with respect to which comparison deviated significantly—whether growth rate was or was not included in the MANOVA, and so only one result set, that including this variable, is presented in this paper (Table 2). There was a highly significant difference in developmental instability, but only between the years. Univariate analysis showed that FA was greater for the El Niño fish with respect to otolith weight and shape, but not width or length (Tables 3 and 4).

To examine the possibility that the between-year differences were not due to El Niño effects, we examined otoliths of 4-year-old fish from another year class (1977) unaffected by El Niño events. As with the above two groups, fish sampling took place during the first two weeks of September. These otoliths were analyzed for right-left asymmetry in weight and shape. Results of a Multiple Analysis of Variance for all three year classes, with fixed effects of year and sex, are given in Tables 5 and 6. The results, in conjunction with Tukey tests for differences among years (Table 7) show clear increases in right-left differences in both shape and weight for the 1980 El Niño year over 1984 and, in shape, over 1977 as well. Differences between the two years not affected by El Niño (1977 and 1984) were not statistically significant.

Table 1

Tests for normality of (L–R)/(L+R) for various traits used in developmental instability. (L indicates measure on the left, R the corresponding measure on the right otolith).

Width of otolith (n = 147)
Mean = 0.002
Skew = 0.184
Kurtosis = 1.333
Shapiro-Wilk W = 0.990
P = 0.9456

Weight of otolith (n = 135)
Mean = 0.003
Skew = 0.242
Kurtosis = 0.683
Shapiro-Wilk W = 0.994
P = 0.9965

Length of otolith (n = 135)
Mean = 0.001
Skew = 0.049
Kurtosis = 2.030
Shapiro-Wilk W = 0.975
P = 0.1981

Growth rate of otolith (1980 year class; n = 79)
Mean = –0.001
Skew = –1.567
Kurtosis = 6.124
Shapiro-Wilk W = 0.981
P = 0.0001

Growth rate of otolith (1984 year class; n = 69)
Mean = 0.002
Skew = –0.281
Kurtosis = 0.248
Shapiro-Wilk W = 0.981
P = 0.7044

Discussion

The observation that only two of the five right-left asymmetry measures responded to stress at a statistically detectable level raises the question of consistency. If developmental instability is to be a useful indicator of stress, we need to know what measures will be relatively sensitive to stress and which will not. Highly

Table 2

Multiple analysis of variance for various traits used in developmental instability analysis. Fixed effects are year, sex and growth rate. Variables are right-left differences in width, weight, length, growth rate, and shape.

Effects	Wilks Lambda	F	df	P
Year	0.8029	5.596	5, 114	0.0001
Sex	0.9509	1.176	5, 114	0.3253
Growth	0.9532	1.119	5, 114	0.3546
Year × sex	0.9407	1.438	5, 114	0.2159
Year × growth	0.9230	1.901	5, 114	0.0995
Sex × growth	0.9612	0.961	5, 114	0.4704
Year × sex × growth	0.9936	0.146	5, 114	0.9807

Table 3

Univariate breakdown of multivariate analysis of variance for various traits used in developmental instability analysis.

Fixed effect	df	SS	*F*	*P*
Variable				
Weight				
Growth rate	1	0.00001	0.26	0.608
Sex	1	0.00009	2.28	0.133
Year	1	0.00036	9.07	0.003
Growth × sex	1	0.00010	2.63	0.107
Growth × year	1	0.00001	0.35	0.554
Sex × year	1	0.00008	2.09	0.151
3-Way	1	0.00002	0.49	0.487
Error	118	0.00469		
Width				
Growth rate	1	0.00000	0.00	0.951
Sex	1	0.00003	0.88	0.350
Year	1	0.00008	2.08	0.152
Growth × sex	1	0.00001	0.32	0.574
Growth × year	1	0.00030	2.54	0.114
Sex × year	1	0.00004	1.15	0.286
3-Way	1	0.00000	0.01	0.930
Error	118	0.00456		
Growth rate				
Growth rate	1	0.00134	4.11	0.045
Sex	1	0.00058	1.77	0.186
Year	1	0.00073	2.24	0.137
Growth × sex	1	0.00000	0.00	0.998
Growth × year	1	0.00068	2.10	0.150
Sex × year	1	0.00067	2.06	0.154
3-Way	1	0.00007	0.22	0.639
Error	118	0.03837		
Shape				
Growth rate	1	0.00065	0.76	0.385
Sex	1	0.00015	0.17	0.679
Year	1	0.01856	21.79	0.000
Growth × sex	1	0.00220	2.58	0.111
Growth × year	1	0.00076	0.89	0.347
Sex × year	1	0.00292	3.43	0.066
3-Way	1	0.00006	0.07	0.753
Error	118	0.10049		
Length				
Growth rate	1	0.00002	0.60	0.440
Sex	1	0.00001	0.31	0.581
Year	1	0.00000	0.00	0.986
Growth × sex	1	0.00002	0.62	0.433
Growth × year	1	0.00009	2.66	0.106
Sex × year	1	0.00001	0.39	0.534
3-Way	1	0.00000	0.01	0.933
Error	118	0.00409		

Table 4

Means of developmental instability indices of Pacific hake *(Merluccius productus)* otoliths for 1980 and 1984 year classes.

	1980 (El Niño Group)		1984 (Non El Niño Group)	
Variable	Males (*n*)	Females (*n*)	Males (*n*)	Females (*n*)
Weight	0.0083 (36)	0.0117 (36)	0.0065 (24)	0.0065 (30)
Shape	0.0831 (36)	0.0950 (36)	0.0679 (24)	0.0603 (30)

Table 5

Multiple analysis of variance over one El Niño year (1980) and two Non-El Niño years (1977, 1984). Fixed effects are year and sex. Variables are weight and shape.

Effects	Wilks Lambda	*F*	df	*P*
Year	0.7606	11.876	4, 324	0.000
Sex	0.9930	0.574	2, 162	0.564
Year × sex	0.9577	1.770	4, 324	0.135

Table 6

Univariate breakdown of multiple analysis of variance for two traits used in developmental instability analysis over three years (1977, 1980, 1984).

Sum of squares		df	*F*	*P*
Variable = weight				
Sex	0.00002	1	0.63	0.430
Year	0.00038	2	5.01	0.008
Sex × year	0.00017	2	2.18	0.116
Error	0.00621	163		
Variable = shape				
Sex	0.00062	1	0.82	0.366
Year	0.03576	2	23.65	0.000
Sex × year	0.00285	2	1.89	0.155
Error	0.12322	163		

Table 7

Tukey test for differences among years (1977, 1980, 1984) in two measures of developmental instability. El Niño year class is 1980; Non El Niño year classes are 1977, 1984. NS = not significantly different.

Year class	Difference between means	(Sample sizes)	*P*
Shape			
1980–1984	0.0250	(77, 59)	<0.05
1980–1977	0.0337	(77, 25)	<0.05
1977–1984	–0.0087	(25, 59)	NS
Weight			
1980–1984	0.0033	(79, 55)	<0.05
1980–1977	0.0024	(79, 38)	NS
1977–1980	0.0009	(38, 55)	NS

Table 8
Means of asymmetry in growth rate for Pacific hake *(Merluccius productus)* in an El Niño and a non-El Niño year.

	Year	
	El Niño (1980)	Non El Niño (1984)
Growth rate		
Slow	0.0142	0.0132
Fast	0.0251	0.0157

canalized traits are unlikely to be sensitive indicators of stress. High phenotypic variance can generally be considered an indication of low canalization, and Zakharov (1989) has shown that, at least for *Lacerta* lizards, FA rises with phenotypic variability (see also Soule, 1967).

A related observation is that traits directly and strongly affecting fitness, i.e., under intense stabilizing selection and, therefore, with low heritability, should be poor candidates for detecting stress (Soule and Cuzin-Roudy, 1982). Similarly, structures whose development is affected by use may not be appropriate for FA analysis. Locomotion, for example, might discourage asymmetric growth of limb size. Long-bone length in laboratory rats shows no FA response to heat, cold, behavioral, or audiogenic stress, while long-bone density, not a size characteristic, does (Doyle et al., 1977).

In choosing measures of developmental instability, it may be useful to consider structural detail. With respect to otoliths, weight, length, width, and growth rate represent growth along a single dimension. These metrics, then, are a simple summation of one or more growth processes. Shape, on the other hand, reflects growth processes whose parts are separably measurable. Thus, shape does not compound and thereby obscure information. We might, accordingly, expect to find differences in the shapes of corresponding right and left structures to be more sensitive indicators of stress than simple metric differences, a prediction consistent with the hake otolith results presented here.

Do natural environmental stressors, as well as man-caused disturbances, result in developmental instability? The results reported here suggest an affirmative answer, namely that while DI might be usefully applied in management, it must be used with caution. Use of fin asymmetries or scale circulus aberrations in comparing hatchery stocks for smolt quality, for example, should involve only a single year class and should be given decreasing consideration as stocks diverge genetically or geographically. Suspected problems arising from water contamination in Puget Sound might be investigated or monitored by examining FA, but only so long as the control population comes also from Puget Sound.

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Abstract.—Analytical and statistical procedures were applied to bottom trawl survey data in tests of hypotheses about potential effects of sewage sludge dumping at a 106-mile dumpsite (106-MDS) off New Jersey on fishery resources assessed on the continental shelf and upper slope. Sludge dumping, even in deep ocean waters, was not discounted as one of several ecological and environmental perturbations influencing these resources measured as temporal, spatial, and seasonal differences in abundance. Species abundances of silver and red hakes (*Merluccius bilinearis* and *Urophycis chuss*), summer flounder (*Paralichthys dentatus*), goosefish (*Lophius americanus*), and black sea bass (*Centropristis striata*) declined significantly over temporal and spatial scales during the disposal of contaminant-laden sewage sludge at the deepwater 106-MDS. There was also a decline in the array of all aggregated species, but to a lesser degree. Results of these analyses of assessment data are considered in relation to effects of ocean dumping in shallow waters at the southern California sewage outfalls and in the New York Bight apex, and in relation to increased contamination of the ecosystem around the 106-MDS. Further, large-scale coordination of environmental research surveys with fishery resource assessments would allow tests of more specific hypotheses and allow a more definitive interpretation of offshore resource population data as presented here.

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Analysis of fishery resources: potential risk from sewage sludge dumping at the deepwater dumpsite off New Jersey

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Sewage sludge and a variety of other wastes have been disposed of in coastal waters of the New York Bight for over 50 years (Squires, 1983). Offshore deepwater waste disposal of sewage sludge, however, is a relatively new activity of the last 20 years. With legally mandated closure of the coastal water 12-mile dump site (12-MDS) in the New York Bight apex (Ocean Dumping Ban Act of 1988), a deepwater dumpsite, 106 miles off New Jersey (106-MDS), was selected as a temporary alternative site for disposal of sewage sludge from the New York and New Jersey metropolitan area (O'Connor, 1983; O'Connor et al., 1983, 1985; Pearce et al., 1983; Norton, 1989; NOAA[1,2]; Battelle[3]).

The 106-MDS had been used previously for disposal of industrial wastes as well as sewage sludge (O'Connor, 1983; Bisagni[4]; Anderson[5]). Phased relocation of New York-New Jersey sewage disposal began in March 1986, and by December 1987 all sewage sludge disposed at sea was being barged to the 106-MDS site. At the 106-MDS, an average of 6.0 million metric tons (t) wet weight sewage sludge (range 1.2–9.9 million t) was dumped between 1986 and 1992. This mean is similar to an average of 5.8 million t of sewage sludge (range 4.0–8.3 t) dumped at the 12-MDS from 1973 to 1987. New Jersey ceased disposal at 106-MDS in March 1991. New York City phased out 20% of its ocean dumping in December 1991, and the remainder by the end of June 1992.

The fishing industry, citizens groups, state governments, and federal agencies all voiced concerns about potential effects of heavy sewage sludge dumping at the 106-MDS on the surrounding marine environment and fisheries. Dumping of sewage sludge and industrial waste in

[1]NOAA. 1975. May 1974 baseline investigation of deepwater dumpsite 106. NOAA Dumpsite Evaluation Report 75-1. U.S. Dep. Commer., Natl. Oceanic Atmospheric Admin., Natl. Ocean Survey, Rockville, MD, 388 p.

[2]NOAA. 1977. Baseline report of environmental conditions in deepwater dumpsite 106. NOAA Dumpsite Evaluation Report 77-1. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, Rockville, MD, 798 p.

[3]Battelle. 1990. 106-miles deepwater municipal sludge site monitoring, research and surveillance plan. Battelle Memorial Institute, Duxbury, MA, 90 p.

[4]Bisagni, J. J. 1977. A summary of the input of industrial waste chemicals at deepwater dumpsite 106 during 1974 and 1975. NOAA Dumpsite Evaluation Report 77-1. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, Rockville, MD, 487–497 p.

[5]Anderson, P. W. 1983. Current status—ocean dumping in the New York Bight. Paper presented on 6 April 1983 in Atlantic City, NJ at the 15th National Conference and Exhibition on Municipal and Industrial Sludge Utilization and Disposal, 6 p.

the comparatively pristine deep-water ocean environment has been considered to have an adverse effect on fishery resource abundance and composition (Carlise, 1969; Dart and Jenkins, 1981; Mearns, 1981; Russo, 1982; Cross et al., 1985; Spies, 1984; Farrington et al., 1982; Capuzzo and Kester, 1987, a and b; O'Connor et al., 1985, 1987, a and b; Werme[6,7]; SCCWRP[8]; Zdanowicz et al.[9]; NMFS[10,11]; Studholme et al.[12]). A contaminant distribution model presented by O'Connor et al. (1985) (see also Reed et al., 1985) indicated that New York and New Jersey sewage sludge has the immediate effect of increasing concentrations of polychlorinated biphenyls (PCB's), Zn, Pb, Cr and Cu. In addition, the potential area of influence (**PAI**) of waste disposal at the 106-MDS extends over a wide region (Fig. 1) off the Middle Atlantic outer continental shelf and upper slope (Bisagni, 1983; O'Connor et al., 1985; Gentile et al., 1989; Warsh[13], Bisagni[14], Ingham[15]).

A change in fish species population abundance and composition is known to have occurred near shallow-water sewage sludge disposal outfalls in southern California (Mearns 1981; Sherwood[16]). For example, a bothid flounder (Pacific sanddab, *Cithaichthys sordidus*) was replaced by a pleuronetcid (Dover sole, *Microstomus pacificus*). Increased growth rates and high prevalence of fin erosion of Dover sole, however, appear to have resulted from exposure to sediments contaminated with chemical wastes from the outfalls. Liver anomalies were noted as well and seem to have been associated with exposure to sludge-related contaminants (Mearns, 1981). Spies (1984) reported that distribution of bottom-feeding fishes (e.g., Dover sole) is probably affected by degraded benthic habitats and abundance of benthic (e.g., polychaete, *Capitella capitata*) and pelagic prey around these outfalls in the southern California Bight. Some chemical contaminants associated with the sewage accumulated at higher trophic levels in predatory fishes, e.g., Pacific sanddab and boccaccio, *Sebastes paucispinis*. Benthic-pelagic coupling was evident in the accumulation of chlorinated hydrocarbons in Dover sole and Pacific sanddab.

Cessation of sewage sludge dumping on the biomass of the most frequently occurring fish species around the coastal waters near 12-MDS from 1986 to 1989 was examined by Studholme et al.[12]. There were no significant changes, although American lobster (*Homarus americanus*) biomass increased (Pikanowski, 1992; Wilk et al.,[17]). Possibly this 39-month-long study period was insufficient to detect a recovery of any finfish species alterations resulting from decades of sewage dumping at the old 12-MDS. Interestingly, the high prevalence of fin-rot disease of winter flounder (*Pleuronectes americanus*) around the 12-MDS reported earlier (Ziskowski and Murchelano, 1975; Murchelano and Ziskowski, 1976) declined significantly after cessation of the dumping (O'Connor et al.[18]; Pacheco and Rugg[19]). It was also shown earlier that Atlantic mack-

[6]Werme, C., R. Shokes, W. Steinhauer, S. McDowell, P. Debrule, P. Hamilton, and P. Boehm. 1988a. Evaluation and recommendations for bioaccumulation studies for the 106-mile deepwater municipal sludge site monitoring program. Battelle Memorial Institute, Duxbury, MA, 36 p.

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[10]NMFS. 1992a. Interim report on monitoring the biological effects of sludge dumping at the 106-mile dumpsite. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole, MA 02543, 128 p

[11]NMFS. 1992b. Second annual report on monitoring the biological effects of sludge dumping at the 106-mile dumpsite. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole, MA 02543, 157 p

[12]Studholme, A. L., J. O'Reilly, and M. C. Ingham (eds.). 1993. Effects of the cessation of dumping at the 12-mile site. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Sandy Hook Lab., Highlands, NJ 07732. (In review.)

[13]Warsh, C. E. 1975. Physical oceanography hist rical data for Deepwater Dumpsite 106. NOAA Dumpsite Evaluation Report 75-1. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, Rockville, MD, 105–140 p.

[14]Bisagni, J. J. 1976. Passage of anticyclonic Gulf Stream eddies through Deepwater Dumpsite 106 during 1974 and 1975. NOAA Dumpsite Evaluation Report 76-1. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, Rockville, MD, 39 p.

[15]Ingham, M. C. 1977. The general physical oceanography of deepwater dumpsite 106. NOAA Dumpsite Evaluation Report, 77-1. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, Rockville, MD, 29–54 p.

[16]Sherwood, M. J. 1978. The fin erosion syndrome. Southern California Coastal Water Research Project. Annual Report 1978, 203–221 p.

[17]Wilk, S. J., R. A. Pikanowski, A. L. Pacheco, D. G. McMillan, and L. L. Stehlik. 1993. Response of fish and megainvertebrates of the New York Bight apex to the abatement of sewage sludge dumping: an overview. *In* A. L. Studholme, J. O'Reilly and M. C. Ingham (eds.), Effects of the cessation of dumping at the 12-mile site. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole, MA, 14 p. (In review.)

[18]O'Connor, J. S., J. J. Ziskowski, and R. A. Murchelano. 1987. Index of pollutant-induced fish and shellfish disease. NOAA Spec. Rep. Ocean Assessment Div. U.S. Dep. Commer., NOAA, Natl. Ocean Survey, Rockville, MD, 29 p.

[19]Pacheco, A. L., and J. Rugg. 1993. Disease incidence of inner New York Bight winter flounder collected during the 12-mile dumpsite study, 1986–1989. *In* A. L. Studholme, J. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of dumping at the 12-mile site. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Sandy Hook Lab., Highlands, NJ, 14 p. (In review.)

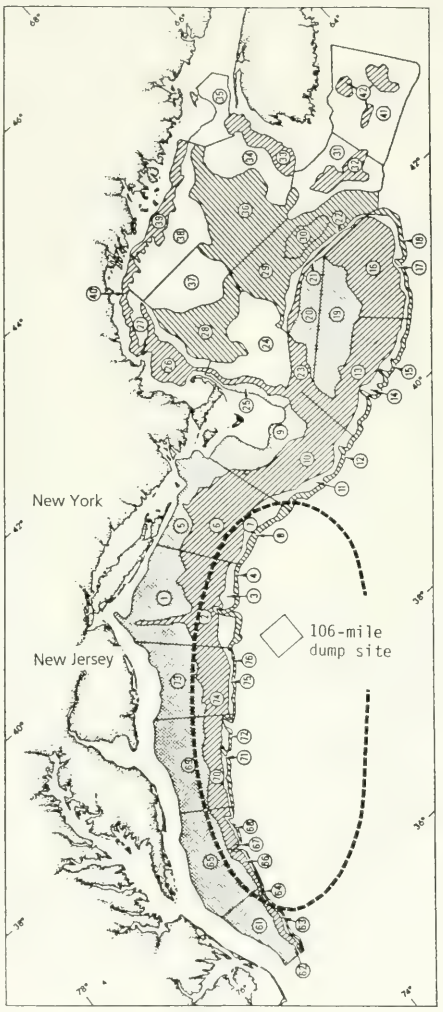

Figure 1

Location of the 106-mile dumpsite and strata used in Northeast Fisheries Science Center bottom trawl surveys (1963 to present). The potential area of influence (PAI) by sewage sludge dumping is within the dashed line, which is adapted from Biasagni (1983).

erel (*Scomber scombrus*) embryos developing in surface waters about the 12-MDS (1974–1978) had greater mortality and gross malformation, more mitotic abnormality and mitotic inhibition than those in less contaminated bight areas, and this was linked to site contamination (Chang and Longwell, 1984; Longwell,1988; Longwell et al., 1992).

Unlike the 12-MDS in the New York Bight apex and the sewage outfalls in southern California, the 106-MDS is situated in a physically dynamic zone characterized by periodic shifts and overturns in water masses. The toxic water is rapidly diluted and dispersed. This may diminish the impact of dumped waste and associated chemical contaminants, but it also makes determination of any adverse effects on the resource more difficult to study than those associated with sewage sludge dumping in shallow-waters. Still, the economic value of the nearby fisheries warrants some effort at directly measuring potential adverse impacts of the 1986–92 sludge dumping on the fishery resource in the vicinity of the 106-MDS.

The study reported here is an attempt to determine if any change in fishery resource abundance on the adjacent continental shelf and slope could be detected after sewage sludge disposal commenced at the 106-MDS in March 1986. Although ocean dumping is now banned, this period of sludge dumping in the deep ocean provides an interesting case study for consideration of effects of ocean pollution in general on economically important fishery resources. This analysis is of potential interest in respect to any future reconsideration of ocean dumping. There are no prior population level studies on abundance changes in marine fishes associated with the sewage sludge dumping in deep ocean waters.

The general null hypothesis that was tested is that no change in resource species abundance and composition was coincident with sewage dumping at the deepwater 106-MDS during the period 1986–90. Assessments were made of temporal, spatial, and seasonal differences in 11 individual finfish

species, and of all these species combined. The general hypothesis was subdivided into three more specific hypotheses, each of which was likewise tested: 1) there are no *temporal* differences in species abundance between the period prior to sewage sludge dumping at the 106-MDS and the period after dumping resumed; 2) there are no *spatial* differences in species abundance between the area north of the 106-MDS and the area south of the dump site, the latter more likely to be influenced by the sewage sludge that supposedly moved through the dump site toward the west-southwest shallow outer shelf (PAI; Fig. 1); and 3) there are no *seasonal* differences for individual and all species for the north and south areas within the pre- and post-dumping periods.

Methods

Data from NOAA's Northeast Fisheries Science Center (NEFSC) bottom trawl surveys were used for analysis. From 1963 to the present, NEFSC has conducted bottom trawl surveys on the Northwest Atlantic Shelf and upper slope, from the Scotian Shoals to Cape Hatteras including the areas adjacent to the 106-MDS (Fig. 1). The entire survey area has been stratified by depth down to 365 m, and surveys have been based on a stratified random design that provides statistically valid samples for estimating indices of species population abundance. All fishes and invertebrates are sorted, counted, and weighed by species to the nearest 0.1 kg. Large catches are subsampled by weight and volume and expanded to estimate the entire catch. Detailed information pertinent to the rationale, descriptions of trawl gears and sampling schemes, as well as history of the NEFSC bottom trawl survey are provided by Grosslein (1974) and more recently Azarovitz (1981). Grosslein et al. (1979) summarized research, assessment, and management of the northwest Atlantic ecosystem using data from NEFSC bottom trawl surveys.

Data from the spring 1982 through spring 1986 NEFSC surveys were evaluated as the pre-dumping period, and data from autumn 1986 through spring of 1990 as the post-dumping period. Eleven economically important species were selected for analysis: silver hake (*Merluccius bilinearis*); red hake (*Urophycis chuss*); summer flounder (*Paralichthys dentatus*); goosefish (*Lophius americanus*); black sea bass (*Centropristes striatus*); scup (*Stenotomus chrysops*); butterfish (*Peprilus triacantus*); longfin squid (*Loligo pealei*); American lobster (*Homarus americanus*); sea scallop (*Placopecten magellanicus*); and spiny dogfish (*Squalus acanthias*). Species were selected on the basis of their commercial values and landings, and the known availability of data for the entire 106-MDS study area (Chang, 1990). In addition, all species, a category comprising the total catch for each cruise, was also used.

The multivariate rank sum test (Puri and Sen, 1971) was employed for temporal, spatial, and seasonal differences in the population abundance analyses by using the catch per unit of effort (CPUE) as a measure of population abundance: 1) the *average* CPUE values for each bottom trawl survey stratum for all cruises occurring in the pre-dumping period cruises (spring 1982–spring 1986), and for all cruises occurring in the post-dumping period cruises (autumn 1986–spring 1990), and 2) the average CPUE data from the area defined as south of the 106-MDS, including strata 61–76 and data from the area defined north of the site including strata 1–12 (Fig. 1). Test statistics for CPUE were calculated and compared with critical values from the chi-square table to determine the following:

1. there are no temporal differences in CPUE of pre- and post-dumping periods for spring and autumn cruises collectively in the regions north and south of the 106-MDS (cf. Table 1),
2. there are no spatial differences in CPUE north and south of the 106-MDS for pre- and post-dumping period cruises collectively in spring and autumn seasons (cf. Table 2),
3. there are no seasonal differences in CPUE of spring and autumn surveys for pre- and post-dumping period cruises collectively in the regions of north and south of the 106-MDS (cf. Table 3).

Test statistics were also computed and compared with the critical values for testing CPUE for spatial differences for individual species and for all species taken on each cruise in the area north and south of the 106-MDS. Test statistics and abundance indices of individual species in tabulated form are not included among tables given here.

The values of test statistics for temporal, spatial, and seasonal differences are readily comparable (Tables 1–3). When examining values of the test statistics for temporal differences, secondary differences for species, regions, and seasons were also assessed. Test statistics were similarly examined for spatial and seasonal differences among species, regions, and seasons.

Changes in significance or non-significance of the test statistics between pre- and post-dumping period surveys may be interpreted as indicative of temporal differences in CPUE. Significant changes of test statistics between regions north and south of the 106-MDS indicate spatial differences. Changes between spring and autumn surveys indicate seasonal differences. Significant differences in CPUE in time, space, and season may thus be interpreted as some shift in species abundance. *Negative* differences are taken here as a response of the population to some adverse

Table 1

Results of the rank sum test for **temporal** differences in species catch per unit of effort (CPUE) between pre- and post-dumping periods using spring and autumn cruises collectively in north and south regions.

	Pre-dumping period vs. post-dumping period					
	Spring Cruises			Autumn Cruises		
Species name	CPUE (weight)	CPUE (number)	No. of species	CPUE (weight)	CPUE (number)	No. of species
North						
Silver hake	0.098	4.709*		2.064	0.621	
Red hake	0.596	0.075		10.087*	3.320	
Summer flounder	8.553*	2.349		1.409	1.817	
Goosefish	2.290	0.001		15.520*	1.192	
Black sea bass	0.423	0.140		0.482	2.964	
Scup	0.127	1.035		7.656*	2.910	
Butterfish	7.288*	11.810*		1.361	0.161	
Longfin squid	0.225	0.039		4.443*	0.001	
American lobster	3.170	0.168		1.184	0.639	
Sea scallop	3.626	5.285*		1.199	1.736	
Dogfish	17.166*	10.993*		0.003	0.094	
All species[1]	10.077*	4.094*	2.503	0.671	0.051	3.278
South						
Silver hake	1.472	0.040		0.966	6.984*	
Red hake	6.391*	4.576*		0.707	0.700	
Summer flounder	6.645*	10.785*		1.219	1.440	
Goosefish	0.934	0.118		3.664	0.033	
Black sea bass	5.207*	6.474*		0.386	0.240	
Scup	1.184	0.077		0.943	0.087	
Butterfish	0.147	0.050		8.443*	12.691*	
Longfin squid	1.801	1.395		2.548	0.327	
American lobster	0.247	2.792		1.713	1.539	
Sea scallop	16.057*	12.614*		0.973	1.600	
Dogfish	0.242	0.043		0.362	1.297	
All species[1]	14.641*	21.212*	1.834	9.099*	2.377	8.473*

[1] "All species" includes the eleven listed and all other species.
* Significant difference with the critical values at 95% level in the chi-square table.

biological or environmental perturbation, to fishing pressure or to some combination of these factors. *Positive* differences are taken as increased species abundance in response to favorable conditions. Nonetheless, significant differences of this sort alone do not establish a direct causal association between change in population abundance and sewage sludge dumping, or alternately between fishing pressure, natural environmental perturbations, or any of combination of these. Any such inference must come from further interpretation of the data in respect to what is known about natural ecology of the subject species, fishing pressure on these, and any known sensitivities to sewage sludge.

Abundance indices for the 11 species individually and for all species combined for pre- and post-dumping period surveys (Tables 4–7, pgs. 601–604) were computed by using the groundfish survey analysis program (Kramer[20]). Basic assumptions and methodology for estimation of abundance indices based on NEFSC bottom trawl survey data are detailed by Pennington and Brown (1981). Trends in indices and variabilities in time and space may also be interpreted as suggesting some general shift in species abundance attributable to sludge dumping, even though there may be no direct proof of an association between population abundance change and sludge disposal.

Results

Temporal differences

Test statistics based on species CPUE, and species abundance indices, including estimates for both spring and autumn cruises, are summarized in Tables 1 and 4–7. Combining the information from these two sources reinforces the inferences of significant change in species abundance over time.

[20] Kramer, W. P. 1985. Groundfish survey analysis program (SURVAN version 5.2), program report. Prepared for U.S. Dep. of Commer., NOAA,. Natl. Mar. Fish. Serv., Northeast Fish. Cent., Input Output Computer Service Inc., Waltham, MA. 137 p.

Table 2

Results of the rank sum test for **spatial** differences in species catch per unit of effort (CPUE) between north and south regions using pre- and post-dumping period cruises collectively in spring and autumn seasons.

	North region vs. south region					
	Pre-dumping cruises			Post-dumping cruises		
Species name	CPUE (weight)	CPUE (number)	No. of species	CPUE (weight)	CPUE (number)	No. of species
Spring						
Silver hake	13.402*	28.189*		17.765*	35.719*	
Red hake	3.654	6.591*		15.014*	22.364*	
Summer flounder	5.833*	5.161*		2.356	0.624	
Goosefish	0.228	0.469		0.467	0.023	
Black sea bass	0.259	0.727		1.956	2.217	
Scup	2.483	1.295		0.511	8.128*	
Butterfish	12.030*	10.791*		0.496	0.154	
Longfin squid	1.201	4.823*		0.004	7.375*	
American lobster	0.160	1.747		2.235	6.298*	
Sea scallop	0.001	0.351		5.503*	4.505*	
Dogfish	16.084*	3.279		0.115	1.561	
All species[1]	1.078	0.943	11.532*	0.113	6.313*	8.808*
Autumn						
Silver hake	40.064*	8.555*		41.868*	24.898*	
Red hake	33.139*	17.622*		11.277*	7.116*	
Summer flounder	11.877*	1.987		12.920*	1.263	
Goosefish	46.468*	4.564*		24.837*	0.819	
Black sea bass	6.133*	2.938		14.058*	0.304	
Scup	0.532	2.283		0.018	0.729	
Butterfish	5.400*	0.062		16.728*	10.153*	
Longfin squid	10.717*	10.898*		5.531*	12.555*	
American lobster	0.178	1.747		0.140	4.371*	
Sea scallop	0.635	1.157		0.288	0.639	
Dogfish	10.896*	3.279		29.296*	18.483*	
All species[1]	24.920*	9.559*	5.992*	50.827*	21.397*	43.765*

[1] "All species" includes the eleven listed and all other species.
*Significant difference with the critical values at 95% level in the chi-square table.

Analyses of red hake data are used here as an example of a detailed interpretation of temporal differences in species CPUE. (Black sea bass could be equally well used because of its similar pattern of CPUE indices.) Species test statistics for red hake revealed significant temporal differences in CPUE indices both by weight (biomass) and number of individuals in the south, but not in the north region (Table 1). Biomass indices declined from pre-dumping spring cruises to post-dumping spring cruises (Table 4). Numerical abundance indices also declined from pre-dumping spring cruises to post-dumping spring cruises (Table 5). Red hake autumn data were also analyzed, but the species test statistics were not significant (Table 1). Biomass indices (Table 6) and number indices (Table 7) declined from the pre-dumping to the post-dumping period. These negative temporal differences for red hake are interpreted as an indication of significant reduction in abundance over time.

CPUE test statistics for several other species also suggest significant temporal differences between pre- and post-dumping periods. The number of significant differences was greater for spring cruises than for autumn cruises (Table 1). Biomass indices were relatively low for both spring and autumn cruises in both north and south regions generally, with the exception of high values for dogfish (Tables 4 and 6). Species number indices were mixed (Tables 5 and 7).

Test statistics for summer flounder and sea scallop CPUE by weight and number for the spring cruises were significantly different in the southern region. In the northern region, only summer flounder biomass and scallop number indices were significantly different. Indices for summer flounder and sea scallop for autumn cruises, however, failed to be significant in either region (Table 1). Summer flounder abundance indices of both biomass and number indicate a decline from the pre-dumping period to the post-dumping period, while both indices for the sea scallop increased (Tables 5 and 7). This suggests a decline (negative differences) over time for summer flounder, and an enhancement (positive differences) for sea scallop.

Table 3

Results of the rank sum test for testing **seasonal** differences in species catch per unit of effort (CPUE) between spring and Autumn seasons using pre- and post-dumping period cruises collectively in north and south regions.

	Spring season vs. autumn season					
	Pre-dumping cruises			Post-dumping cruises		
Species name	CPUE (weight)	CPUE (number)	No. of species	CPUE (weight)	CPUE (number)	No. of species
North						
Silver hake	1.444	1.473		8.382*	2.653	
Red hake	8.745*	4.845*		0.057	0.291	
Summer flounder	5.024*	0.471		8.835*	1.378	
Goosefish	0.098	4.898*		3.337	0.681	
Black sea bass	6.519*	2.850		8.597*	0.009	
Scup	0.078	2.757		2.498	6.681*	
Butterfish	1.123	0.945		6.645*	14.920*	
Longfin squid	9.991*	21.686*		0.262	14.070*	
American lobster	0.988	0.033		4.137*	0.683	
Sea scallop	4.774*	4.137*		1.490	0.806	
Dogfish	11.294*	4.527*		20.414*	16.008*	
All species[1]	15.317*	41.133*	1.944	57.442*	22.629*	0.265
South						
Silver hake	35.795*	2.322		27.903*	2.594	
Red hake	6.125*	0.291		0.707	0.108	
Summer flounder	0.035	0.150		0.002	0.045	
Goosefish	28.811*	0.509		16.162*	0.131	
Black sea bass	3.476	0.506		10.751*	4.645*	
Scup	6.210*	3.409		0.019	0.085	
Butterfish	4.236*	16.741*		0.292	0.742	
Longfin squid	3.229	0.342		0.762	3.974*	
American lobster	0.095	5.804*		0.013	0.689	
Sea scallop	6.425*	4.257*		0.289	0.206	
Dogfish	16.927*	8.076*		53.442*	37.763*	
All species[1]	51.240*	12.546*	0.919	140.185*	7.022*	24.325*

[1] "All species" includes the eleven listed and all other species.
* Significant difference with the critical values at 95% level in the chi-square table.

Biomass and number test statistics for butterfish in spring cruises were significantly different between pre- and post-dumping periods in the northern region, but not significantly different in the southern region. Conversely, those statistics from autumn cruises were not significant in the northern region, but significant in the southern region. Test statistics for spiny dogfish showed similar patterns (Table 1). Species abundance indices for butterfish and spiny dogfish fluctuated, but generated much higher values for the test statistics than did those of other species (Tables 4–7). Accordingly, interpretation of the butterfish and spiny dogfish statistics suggests a positive difference in these two species over time.

In spring cruises, test statistics in CPUE both by weight and number for goosefish, scup, longfin squid, American lobster, and silver hake were not significantly different for pre- and post-dumping periods for either the north or south region, with exception of silver hake number indices in the north region. For autumn cruises, however, there were significant differences between pre- and post-dumping periods for goosefish, scup, and longfin squid (Table 1). Abundance indices for goosefish declined from the pre- to the post-dumping period for both cruises and regions. Longfin squid indices declined from the pre to the post period in spring cruises, but increased in autumn cruises. All scup indices declined but increased in autumn cruises within the south region. American lobster indices showed little change between pre- and post-dumping periods. Silver hake indices increased in spring cruises but declined in autumn cruises from the pre to post period (Tables 4–7). The lower abundance indices of these species may signify that the populations responded negatively to adverse differences.

In spring cruises, CPUE statistics for all species, both by biomass and number, were significantly different between pre- and post-dumping periods in both regions. This occurred though test statistics for some individual species were significantly different and

Table 4

Species abundance indices (e.g., mean and SSE [standard error]) based on **weight** of stratified catch per tow and variabilities (CV in %) using pre- and post-dumping spring cruises collectively in north and south regions.

Species name	Pre-dumping spring cruises			Post-dumping spring cruises		
	Abundance indices			Abundance indices		
	Mean	SSE	CV (%)	Mean	SSE	CV (%)
North						
Silver hake	1.529	0.62509	41	1.217	0.31258	26
Red hake	1.549	0.78584	51	0.863	0.23815	28
Summer flounder	0.401	0.09030	23	0.211	0.05036	24
Goosefish	1.109	0.28732	26	0.656	0.14389	22
Black sea bass	0.104	0.05443	52	0.025	0.01060	42
Scup	0.510	0.23137	45	0.192	0.09896	52
Butterfish	1.820	1.03770	57	0.383	0.13748	36
Longfin squid	1.009	0.27199	27	2.038	0.55665	27
American lobster	0.440	0.19855	45	0.350	0.09429	27
Sea scallop	0.194	0.09369	48	0.877	0.38851	44
Dogfish	51.186	14.36400	28	115.671	36.00800	31
All spp.[1]	183.027	23.42700	13	259.398	38.04700	15
South						
Silver hake	0.426	0.14559	34	0.389	0.10256	26
Red hake	0.671	0.31264	47	0.147	0.06884	45
Summer flounder	0.413	0.10370	25	0.260	0.06533	25
Goosefish	0.938	0.33040	35	0.367	0.17910	49
Black sea bass	0.238	0.08226	20	0.429	0.22193	52
Scup	0.635	0.46357	73	1.293	0.61669	48
Butterfish	0.340	0.15347	45	0.682	0.36380	53
Longfin squid	0.811	0.20697	26	2.382	0.86509	36
American lobster	0.082	0.02381	29	0.151	0.07966	53
Sea scallop	0.092	0.03275	36	1.245	0.73640	59
Dogfish	92.764	36.88800	40	74.456	15.59700	21
All spp.[1]	226.566	53.61400	24	181.878	18.19100	10

[1] "All species" includes the eleven listed and all other species.

others not. In the autumn cruises, biomass statistics were statistically significant between pre- and post-dumping period cruises, but for the southern region only (Table 1). These results substantiate the negative temporal differences. They suggest a reduction over time for all species abundance and biomass in both regions of the study area.

Abundance indices for all species in spring cruises decreased from the pre- to the post-dumping periods but increased in autumn cruises. Variabilities for all species were consistently lower (9–24%) than those for individual species (18–88%) (Tables 4–7). This suggests that fluctuations in total biomass in the study area from 1982 to 1990 for all species were lower as a whole and masked fluctuations in individual species. One may infer that the impacts of fishing, ecological perturbations, or natural factors acting on all species as a whole, therefore, were relatively low in the spring. Although impact on the abundance indices for all species was less than on some individual species, there were no significant differences in the number of species between pre- and post-dumping periods in either region.

Spatial differences

To assess spatial differences for species CPUE between north and south regions, the same approach was used as for temporal differences. Test statistics for spatial differences are summarized in Table 2 and Tables 4–7. These are based on species CPUE, species abundance indices, and their variability estimates from collective cruises in pre- and post-dumping periods.

More species test statistics for autumn cruises were significantly different between the north and south

Table 5

Species abundance indices (e.g., mean and SSE [standard error]) based on **number** of stratified catch per tow and variabilities (CV in %) using pre- and post-dumping spring cruises collectively in north and south regions.

Species name	Pre-dumping spring cruises			Post-dumping spring cruises		
	Abundance indices			Abundance indices		
	Mean	SSE	CV (%)	Mean	SSE	CV (%)
North						
Silver hake	7.143	1.66440	23	9.255	2.13410	23
Red hake	6.491	2.35950	36	5.298	1.52160	29
Summer flounder	0.591	0.12461	21	0.350	0.07453	21
Goosefish	0.410	0.08432	21	0.285	0.05213	18
Black sea bass	0.410	0.23043	56	0.101	0.05330	58
Scup	3.027	1.76110	58	0.574	0.31650	55
Butterfish	28.105	13.54800	48	9.375	4.93800	53
Longfin squid	17.936	5.27820	29	37.478	15.55800	42
American lobster	0.995	0.46534	47	0.897	0.27397	31
Sea scallop	3.214	1.77760	55	35.384	23.24100	66
Dogfish	49.555	16.10700	33	79.592	22.47900	28
All spp.[1]	511.574	48.78400	10	554.673	51.95500	9
South						
Silver hake	2.431	0.57454	24	4.874	1.80180	37
Red hake	2.311	0.79196	34	0.641	0.21119	33
Summer flounder	1.016	0.31625	31	0.760	0.18100	24
Goosefish	0.314	0.07206	23	0.147	0.04088	28
Black sea bass	0.816	0.26722	33	2.007	0.71847	37
Scup	21.419	18.81900	88	17.119	8.51020	50
Butterfish	11.695	6.16760	53	51.810	44.22500	85
Longfin squid	50.430	21.27200	42	119.842	57.41000	48
American lobster	0.133	0.03483	26	0.137	0.04451	32
Sea scallop	1.845	0.62564	34	25.703	17.49900	68
Dogfish	45.598	16.41000	36	39.621	7.73790	20
All spp.[1]	450.046	47.42500	11	675.431	70.50500	10

[1] "All species" includes the eleven listed and all other species.

regions than those for spring cruises (Table 2). Several patterns are evident in significant test statistics for the autumn cruises. Biomass CPUE for eight species showed highly significant differences for both pre- and post-dumping periods. These species were silver hake, red hake, summer flounder, goosefish, black sea bass, butterfish, longfin squid, spiny dogfish, and all species. Fewer significant differences were observed in the number of CPUE. No distinct pattern was obvious for spring cruises. Only silver and red hake CPUE showed significant test statistics for both periods. Scup, American lobster, and sea scallop CPUE showed generally lower values that were not significantly different. There was a significant difference between north and south in number of species for autumn cruises in both the pre-dumping and post-dumping periods (Table 2).

Interpretation of these significant spatial differences requires special caution. In 1982, the first year for which data were used in this study, populations were not of comparable size in the north and south regions. One must consider how populations of unequal size could have accommodated differing environmental perturbations and fishing pressure in the north and south regions. Silver hake, red hake, butterfish, and spiny dogfish indices were highest. Goosefish and American lobster indices were lower overall, but higher in the north than in the south, while scup were higher only in the south. Longfin squid indices were consistent with its migratory pattern (concentrated in the south in spring and in the north in autumn) (Tables 4–7). Test statistics of all eight species were significantly different between north and south (Table 2).

Test statistics were tabulated for species CPUE between north and south, and for species abundance indices, including all species in the north and south regions for individual cruises, but are not presented here. This information supplemented the findings from collective cruises (Tables 2, 4–7). Indices from individual cruises

Table 6

Species abundance indices (e.g., mean and SSE (standard error)) based on **weight** of stratified catch per tow and variabilities (CV in %) using pre- and post-dumping autumn cruises collectively in north and south regions.

Species name	Pre-dumping spring cruises			Post-dumping spring cruises		
	Abundance indices			Abundance indices		
	Mean	SSE	CV (%)	Mean	SSE	CV (%)
North						
Silver hake	1.573	0.31258	23	0.997	0.30246	31
Red hake	2.707	0.69497	26	0.380	0.09313	25
Summer flounder	0.328	0.08221	25	0.135	0.06060	45
Goosefish	1.539	0.34043	22	0.350	0.10007	29
Black sea bass	0.010	0.00598	60	0.005	0.00363	73
Scup	0.905	0.40331	45	0.203	0.07233	36
Butterfish	9.356	3.27910	35	7.924	2.74850	35
Longfin squid	7.771	2.77170	36	4.266	0.94622	22
American lobster	0.539	0.10552	20	0.630	0.11589	18
Sea scallop	0.284	0.10900	38	1.810	1.07450	59
Dogfish	53.835	32.34200	60	19.980	13.61500	68
All spp.[1]	129.958	21.28800	16	76.576	7.16770	9
South						
Silver hake	0.178	0.05286	30	0.060	0.01787	30
Red hake	0.225	0.11908	53	0.052	0.02049	39
Summer flounder	0.439	0.16250	37	0.072	0.02495	34
Goosefish	0.111	0.03029	27	0.032	0.01329	42
Black sea bass	0.082	0.04975	61	0.060	0.02440	41
Scup	1.779	1.05160	59	4.660	3.96680	85
Butterfish	2.605	1.04430	40	2.803	1.43660	51
Longfin squid	2.716	0.64098	24	1.433	0.35703	25
American lobster	0.125	0.02937	24	0.069	0.02283	33
Sea scallop	0.278	0.14392	52	1.126	0.50005	44
Dogfish	0.006	0.00351	59	0.022	0.00672	31
All spp.[1]	65.832	11.32200	17	44.661	9.18910	21

[1] "All species" includes the eleven listed and all other species.

provided insights into how individual fish and shellfish populations responded in time and space. The variabilities were relatively consistent in both regions, despite confounding biotic and abiotic factors. Fluctuations of total biomass for eleven individual species, and for all species as a whole, were relatively stable in both north and south regions during the period 1982–90.

Seasonal differences

Seasonal differences between spring and autumn were determined by the same method used to evaluate temporal and spatial differences. Test statistics for seasonal differences based on species CPUE and species abundance indices with their variability estimates were drawn from collective cruises of the pre- and post-dumping periods. They are summarized in Tables 3 and 4–7.

Species test statistics for the pre-dumping cruises showed more significant differences between spring and autumn seasons than did post-dumping cruises. Weight test statistics provided more significant differences than those based on number. Spiny dogfish CPUE revealed significant test statistics for all categories. Test statistics for black sea bass, based on both biomass and number, showed significant differences between seasons for the post-dumping cruises in the southern region, but not for the pre-dumping cruises in the same region. Similarly, silver hake, butterfish, and American lobster indices in the northern region were significantly different for the post-dumping cruises, but not significantly different for pre-dumping cruises (Table 3). Some species weight abundance indices declined from the pre-dumping to post-dumping periods for both spring and autumn seasons (Tables 4 and 7). These included silver and red hakes, summer flounder, goosefish, and black sea bass. Number of species for the post-dumping cruises in the southern region was also significantly different (Table 3).

Table 7

Species abundance indices (e.g., mean and SSE [standard error]) based on **number** of stratified catch per tow and variabilities (CV in %) using pre- and post-dumping autumn cruises collectively in north and south regions.

Species name	Pre-dumping spring cruises			Post-dumping spring cruises		
	Abundance indices			Abundance indices		
	Mean	SSE	CV (%)	Mean	SSE	CV (%)
North						
Silver hake	32.869	9.57110	29	16.073	4.51730	28
Red hake	13.974	3.72120	27	2.968	0.72162	24
Summer flounder	0.268	0.07093	26	0.135	0.05503	41
Goosefish	0.658	0.13661	21	0.334	0.07429	22
Black sea bass	0.530	0.24114	46	0.137	0.05997	44
Scup	9.652	3.80610	39	7.770	5.12530	66
Butterfish	191.717	60.39400	32	241.977	87.52200	36
Longfin squid	307.679	141.09000	46	297.160	92.28000	31
American lobster	1.245	0.24816	20	1.573	0.30140	19
Sea scallop	4.165	1.58340	30	39.042	25.79400	66
Dogfish	32.848	18.35200	56	13.260	8.71090	66
All spp.[1]	1481.352	162.12000	11	1365.058	154.03000	11
South						
Silver hake	8.632	2.41370	28	3.340	1.03060	31
Red hake	1.436	0.65891	46	0.482	0.19790	41
Summer flounder	1.136	0.40306	22	0.200	0.06627	33
Goosefish	0.252	0.05769	23	0.128	0.03517	27
Black sea bass	1.003	0.62278	62	0.823	0.36718	45
Scup	40.626	24.08400	59	149.944	132.31000	88
Butterfish	85.958	32.22600	37	84.561	47.39100	56
Longfin squid	107.343	33.92100	32	74.365	38.98300	52
American lobster	0.152	0.03600	24	0.142	0.04323	30
Sea scallop	5.443	3.00540	55	22.849	9.84010	43
Dogfish	0.039	0.02346	60	0.131	0.03651	28
All spp.[1]	842.080	117.52000	14	815.743	133.00000	16

[1] "All species" includes the eleven listed and all other species.

Discussion

Analyses of fisheries abundance data, based on catch per unit of effort (CPUE) of NOAA's Northeast Fisheries Science Center (NEFSC) bottom trawl surveys, indicate that abundances of silver hake, red hake, summer flounder, goosefish, and black sea bass declined about the 106-mile dumpsite (106-MDS) from spring of 1982 through spring of 1990. These declines are concurrent with the temporary dumping there of sewage sludge from the New York and New Jersey metropolitan area. Changes in total abundance and biomass for all species combined occurred to a lesser degree because of increased abundance of spiny dogfish, skates (*Raja* spp.) and some pelagic species (e.g., Atlantic mackerel) (NMFS 1991, 1992). There were statistically significant, temporal differences in average abundance values for some individual species and for all species based on spring and autumn bottom trawl surveys within the north and south dumpsite areas. It is particularly worth noting that much of the abundance decline occurred in the south area of the dumpsite. The south region is most likely to be influenced by sewage sludge introduced in waters passing toward the west-southwest shallow outer shelf through the dumpsite in the potential area of influence (**PAI**) of the sewage sludge (Fig. 1; Bisagni, 1983; O'Connor et al., 1985; Gentile et al., 1989; Ingham[15]; Warsh[13]; Bisagni[4]). There were also statistically significant spatial differences in average abundance of many individual species and all species sampled on the spring and autumn surveys within the pre- and post-dumping period at the 106-mile dumpsite. There were seasonal differences, as well, in average values for sev-

eral individual species and all species for north and south areas at the site, and within the pre and post sludge dumping periods.

The hypothesis that fishery resource abundance in the vicinity of the 106-MDS and adjacent outer continental shelf waters was not affected by sewage sludge dumping there from 1986 to 1990 is thereby rejected. Also rejected are the three secondary hypotheses related to the primary one. The likelihood remains that waste disposal, even in deep-ocean waters, has measurable adverse impacts on the resource abundance, at least in the area of direct influence of the toxic waste.

Analysis of survey data alone, however, does not establish cause and effect. It is necessary to consider the likelihood that events neither directly nor indirectly related to sewage sludge dumping at the 106-MDS could have led to the measured decline in abundance and shift in species composition within the study period. Also, it is necessary to consider how an abundance shift could have occurred through sludge dumping within this period of time.

Fishing is foremost among factors affecting fishery resource abundance and species composition unrelated to any effect of ocean disposal of toxic waste. Impacts of fishing pressure on the species sampled at the offshore dumpsite and analyzed in this study are poorly known. There are also other poorly understood natural factors affecting species population abundance around the 106-MDS in the PAI and elsewhere that could have influenced abundance and species composition at this site over the period of the study reported here. These include shifts in spawning time and area, size of predator stocks, decline in size of the spawning biomass, and increase in early life mortality (Gross, 1976; Hempel, 1978; Mayer, 1982; Cross et al., 1985; Tiews, 1985). The dramatic reductions in stock size affected by powerful modern fishing techniques, however, through sheer reduction in stock size, may influence all these factors so that their fluctuation is no longer entirely natural. These same natural factors are likewise potentially affected by ocean dumping of toxic waste as evidenced in the environmental literature (Carlise, 1969; Gross, 1976; Mearns, 1981; Mayer, 1982; Spies, 1984; Wolf and O'Connor, 1988; Champ and Park, 1989; Hood et al., 1989; Baumgartner and Duedall, 1990; Longwell et al. 1992; Longwell[21]; Young and Mearns[22]; NMFS[10,11]; Studholme et al.[12]). Changes in water mass patterns and global warming are possibly the only phenomena not potentially influenced by ocean dumping. Given the complexity of natural and anthropogenic forces acting on populations, existing data sets from fishery ecology are simply not sufficiently synoptic or complete enough to be useful in sorting out direct sludge dumping effects from natural or pseudo-natural processes driving population fluctuation.

Oceanographic dynamics around the 106-MDS make it unlikely that any change in harvestable fishery resources or catch composition could be the result of direct mortality attributable to the sewage since relocated sludge dumping began there in 1986. There is some evidence from embryo studies of planktonic eggs collected in the wake of sludge and acid waste disposal at 106-MDS that direct kills of floating fish eggs can occur, but this dumpsite is not a significant spawning grounds for resource species (Longwell[21]).

Changes in fishery resource abundance at 106-MDS could, however, have been affected by a change in fish behavior in response to dumped material as well as to natural environmental perturbations (Olla et al., 1980). Migration to other areas to escape sludge disposal and its aftermath or to search for other feeding grounds is likely to alter the time and place of spawning and subsequent early-life survival.

Reduced reproductive success and recruitment resulting from increased baseline contaminant body burdens of spawners is another mechanism whereby the population changes measured in the study presented here could have resulted from sludge dumping (Cross and Hose, 1988; Longwell et al., 1992). Offshore contamination of fish has the same potential of affecting subsequent spawning and recruitment as does contamination in nearshore waters and on the spawning grounds. Shifts in species composition could have come about if predator or competitor, or both, species were more tolerant of the sludge than were the resource species. In addition, poor quality eggs could have resulted from inadequate maternal nutrition if there was much direct prey mortality or pollution-impaired reproduction of prey organisms in the wake of the sludge. Contaminant burdens of the reproductive tissues or ripe eggs of the species analyzed in this study are unknown. Extrapolation and formal treatment of existing data on muscle and liver tissues of these or on the reproductive tissues of other species are probably not worthwhile. Contaminant burdens of mature winter flounder eggs alone (Calabrese et al.[23]) suggest that

[21]Longwell, A. C. 1981. Cytological examination of fish eggs collected at and near 106-Mile Site. *In* NOAA Special Report. Assessment Report on the Effects of Waste Dumping in 106-Mile Ocean Waste Disposal Site. Dumpsite Evaluation Report 81-1. U.S. Dep. Commer., NOAA, Office of Mar. Pollution Assessment. Rockville, MD, 257–276 p.

[22]Young, D. R., and A. J. Mearns. 1978. Pollutant flow through food web. Southern California Coastal Water Research Project. Annual Report 1978, 185–202 p.

[23]Calabrese A., A. C. Longwell, and F. P. Thurberg. 1989. Final report on early reproductive success of winter flounder from Boston Harbor with comparisons made to Long Island Sound. Prepared for U.S. Environmental Protection Agency. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Milford Lab., Milford, CT, 61 p.

safety margins for adverse reproductive effects of several contaminants (Susani, 1986; Sorenson, 1991) on fish species at the 106-MDS could easily have been exceeded. Only moderate concentrations of chlorinated hydrocarbons have been shown to be associated with detrimental reproductive effects (Susani, 1986; Westernhagen et al., 1989).

An interdisciplinary effort was made to determine changes in contaminant burdens of fish at the 106-MDS once sludge dumping began (NMFS[10,11]). In 1991, concentrations of metals were relatively low in the epibenthic megafauna species of deepwater fishes, such as blue hake (*Antimora rostrata*), rattails (*Coryphaenoides carapinus* and *C. armatus*), halosaur (*Halosauropsis macrochir*) and commercially valuable slope-dwelling tilefish (*Lopholatilus chamaeleonticeps*), shrimp (*Nematocarcinus ensifer* and *Glyphocrangon sculpta*), and American lobster (*Homarus americanus*). This was generally true for American lobster, with the exception of elevated liver Cd, which could reflect its trans-shelf migration and possible exposure to coastal pollution. Finfishes, however, generally contained relatively high concentrations of chlorinated pesticides and total PCB's in their livers (NMFS[10,11]). Significantly elevated levels of several metals (Ag, Cu,and Cr) were found in midwater myctophids (e.g., *Benthosema glaciale*, *Lobianchia dofleini*, *Ceratoscopelus maderensis*, and *Hygophum hygomii*) at stations southwest of the 106-MDS in the principal area of influence of the sludge.

Plankton (primarily copepods) provide a pathway for entry of potentially toxic chemical contaminants from the sludge into the ocean food-web, because it constitutes the main prey of smaller midwater fishes. Concentrations of metals in plankton samples taken in 1991 were comparable to, or higher than, those observed in fishes collected in 1989. The geographic distributions of metal concentrations in 1991 fishes and plankton suggest that the elevated levels of metals found in certain samples are probably attributable to dumping activity at the 106-MDS. Boehm (1983), however, postulated that offshore, southerly transport of organic contaminants along the New Jersey shore and down-valley transport from the New York Bight apex caused increased metal contaminants. Organic contaminants (PCB's, polynuclear aromatic hydrocarbons (PAH's) and pesticides) were present in lower concentrations in zooplankton than in midwater fishes (NMFS[10,11]).

The highest concentration patterns of PAH's, PCB's, and Ag in the sediment surface layer (0–0.5 cm) tended to follow the distribution patterns of spores of *Clostridium perfringens* (a bacterial indicator of sewage) in sediments collected from depths of 100 to 2800 m in the vicinity of the 106-MDS. *Clostridium perfringens* counts declined gradually to the southwest. Surface sediments were not detectably contaminated with other trace metals. Organic contaminant concentrations in sub-surface strata (0.5–3.5 cm) were higher than in the sediment or deeper layers. Artifacts in sediment cores in the 106-MDS tend to confirm that chemical concentration is related to dumping. All data imply that material dumped at the 106-MDS reached the seabed in the area southwest of the site in the PAI. Data imply that the chemicals associated with the sludge entered the food-web around the dumpsite in the area believed to have been under principal influence of the sludge (NMFS[10,11]). This is the area accounting for the most of the decline in fish species measured in this study.

Unless absorbed by particles or precipitated by other constituents in the water column, slowly sinking wastes must take a long time to reach the bottom because of the great water depth. This increases the likelihood of significant ingestion of waste and associated contaminants by mid-water column prey species of resource fish. Deepwater food-web dynamics have been explored in the 106-MDS by Van Dover et al. (1992) by using the natural stable isotopes of organic carbon nitrogen and sulphur in sewage sludge to trace sewage-oriented organic matter. Organic matter from the sludge was found to reach the deep-sea floor and enter the benthic food-web through consumption by surface-deposit feeders, including a sea urchin (*Echinus affinus*) and a sea cucumber (*Benthodytes sanquinolenta*). Other surface-deposit feeders, including infaunal benthic species such as polychaetes and molluscs, probably also ingest this organic matter contributing to sludge impacts in the open ocean via food-chain dynamics.

There are strong associations of benthic macrofauna with habitat types and sediment contaminants in the continental shelf of the New York Bight (Chang et al., 1992). Species most common in the contaminated area around 12-MDS were mainly polychaetes (e.g., *Tharyx acutus*, *Nephtys incisa*, *Pherusa affinis,* and *Capitella* spp.), as well as a nemertean (*Cerebratulus lacteus*), an anemone (*Ceriantheopsis americanus*), a phoronid (*Phoronis architecta*) and the nut clam *Nucula proxima*. Another group of species was consistently associated with minimally contaminated sediments and appeared to represent a basic natural benthic macrofaunal assemblage for the typical sandy habitat of the Bight shelf. This group included the sand dollar (*Echinarachnius parma*) and several species of amphipods (e.g., *Byblis serrata*, *Corophium crassicorne,* and *Ampelisca agassizi*), as well as polychaetes (e.g., *Goniadella gracilis* and *Exogone hebes*). The roles of these contaminant-sensitive and insensitive species within

certain food-web dynamics for commercially important fisheries resources in the New York Bight are becoming known (Steimle, 1985; Steimle and Terranova, 1991). Chemical analyses of sediment cores tend to confirm that sediment chemical concentration around the 12-MDS is related to some types of dumping, and that sediment concentrations decrease appreciably in some areas 20 months after cessation of sewage sludge dumping (Zdanowicz et al., 1993[24]). Distribution of the contaminant-sensitive and insensitive benthic invertebrate species assemblages in the New York Bight (Chang et al., 1992) then imply that material dumped at the 12-MDS reached the bottom in the area where it was dumped, entered the food-web at the lower trophic levels of benthic organisms, and ascended to the higher trophic levels of predatory fish species (Steimle et al.[25,26]). Similar food-web dynamics could have influenced the temporal and spatial differences in abundance of commercially important species measured in the principal area of sludge influence at the 106-MDS.

Conclusions

Effects of sewage sludge dumping even in the deep ocean at the 106-MDS, like sludge dumping at the 12-MDS in the New York Bight and release of sewage from outfalls in southern California outfalls, cannot be excluded as a factor measurably affecting fishery resource abundance and composition. Natural factors may have caused the population fluctuation assessed around the 106-MDS, but there are no adequate data sets for testing the likelihood that such phenomena, and not deepwater dumping, are responsible. Data sets are even more inadequate for measuring interactive effects of dumping, fishing, and natural phenomena, which must certainly occur. On the other hand, there are identifiable mechanisms by which changes in abundance and composition of fishery resources could have come about in relatively few years as a result of sludge dumping after prior years of industrial and chemical waste disposal at this deepwater site. Increased contamination of the food-web and environment could well have directly and indirectly, possibly differentially, affected both behavior and reproduction of ecologically linked species leading to the unfavorable temporal, spatial, and seasonal differences of the fishery resources around the 106-MDS.

Analyses of bottom trawl surveys and fishery landings data in relation to environmental pollution are of increasing importance as efforts are made to measure any impact of toxic contaminants on fishery resource. The influence of natural and man-induced environmental factors, such as waste dumping, on fishery resources can be treated as concomitant variables (Thomas et al., 1976; Butler and Schutzman, 1979; Marking and Kimerle, 1979; Geyer, 1981, a and b; Reed et al., 1985; Miller et al., 1988; Wallace et al., 1988; Stoddard and Walsh, 1988; Connor, 1989; Gift et al., 1989; Stanford and Young, 1988, Furness and Rainbow, 1990; Word et al., 1990; Manning, 1991). Interpretation of fishery assessment data in relation to the sewage sludge dumping at the 106-MDS, as developed in the discussion above, makes clear that future efforts in all these regards would benefit from better and updated baseline data on the fishery resources. If there were food-web dynamics data as well as more behavioral and reproductive data on responses of marine fish to contaminant levels known to occur in the ecosystems of concern, we would then be better able to understand and determine causal factors influencing species abundance and fishery resources in the vicinity of the 106-MDS and adjacent continental shelf waters. Much is still to be learned about both the natural fluctuation of environmental factors that influence species abundance and population dynamics and about anthropogenic effects on the natural environment. A better understanding of natural and man-induced effects on fishery resources is necessary to minimize adverse controllable impacts on fisheries resources and requires further synthesis of environmental and fishery assessments.

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Abstract.—We examined the average age at attainment of sexual maturity (ASM) and several other reproductive parameters for evidence of density compensatory responses in two stocks of the spotted dolphin, *Stenella attenuata*. The northern offshore and southern offshore stocks were compared because both have been exploited by the yellowfin tuna purse-seine fishery, but at different rates. We predicted decreasing trends in the ASM and increasing trends in the pregnancy rate for each stock because both have declined in abundance. A lower ASM and a higher pregnancy rate were predicted for the sample from the northern offshore stock because it has been exploited to a greater extent than the southern offshore stock. No statistically significant trends were found in the ASM, but the increase in the proportion of sexually mature females simultaneously pregnant and lactating for the northern offshore stock and the decrease in the proportion of mature females in the population for the southern offshore stock over time were statistically significant. The mean estimate of ASM was significantly higher for the northern offshore stock, 11.1 years (SE=0.236), than for the southern offshore stock, 9.8 years (SE=0.264). No significant differences between stocks were found in the mean estimates of reproductive parameters. Our analyses of temporal trends in several biological parameters did not provide conclusive evidence for compensatory responses having occurred, and therefore some possible explanations are considered.

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Comparison of age at sexual maturity and other reproductive parameters for two stocks of spotted dolphin, *Stenella attenuata*

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As population abundance declines, compensatory responses, such as increases in survival and pregnancy rates and a decrease in the average age at attainment of sexual maturity (ASM), are thought to occur (Eberhardt, 1977; Eberhardt and Siniff, 1977). Each situation must be carefully evaluated to determine whether compensatory responses will be detected because the magnitude of the parameter response and the range of population densities over which measurements are made are likely to be species specific, environmentally variable, and subject to parameter measurement error (Goodman, 1981; Fowler, 1981, 1988; DeMaster, 1984a; York, 1987). For species that are difficult to observe, unbiased estimates of survival rates are difficult to obtain, precluding their use as potential biological indices (Barlow and Boveng, 1991). Reproductive rates, however, are generally more easily measured and, if their relationship to population density is determined, may provide indices of compensatory responses for populations (Perrin and Donovan, 1984). For instance, Barlow (1985) reported that in the spotted dolphin (*Stenella attenuata*), the fraction of mature females pregnant, and the fraction of mature females simultaneously pregnant and lactating, may correlate well with per capita resource availability because these parameters were found to be relatively free of collection biases. The identification of biological indices (i.e., biological parameters that correlate with population abundance) would provide a useful management tool to distinguish between trends in population abundance resulting from exploitation or changes in environmental conditions (Hanks, 1981; Gerrodette and DeMaster, 1990).

The spotted dolphin is an ideal choice for this analysis because a lengthy time series of biological and population abundance data are available. This species is used as a cue by purse-seine vessel operators to find yellowfin tuna in the eastern tropical Pacific (ETP) (Perrin, 1969). Dolphins are incidentally killed during fishing operations, and the spotted dolphin population has had the largest number of animals killed in almost every year since 1959 (Smith, 1983; DeMaster et al., 1992). Two stocks of spotted dolphin, the northern offshore and southern offshore stocks, are recognized as separate management units in the ETP (Perrin et al., 1985). During the first decade of the purse-seine fishery, the 1960's, the large numbers of dolphins killed caused the abundance of these two stocks to decline. The northern offshore spotted dolphin was estimated to be between 35% and 50% of their pre-exploitation abundance (circa 1959) by 1979 (Smith, 1983), while the southern offshore stock was estimated to be at 92–98% of its

pre-exploitation size (circa 1973) in 1979 (Smith[1]). Since 1976, both stocks of spotted dolphin are believed to have declined significantly in abundance (Anganuzzi et al., 1992).

As potential biological indices, we estimated ASM and associated reproductive parameters for two stocks of the spotted dolphin. Although for long-lived mammals, like the spotted dolphin, population growth rates are relatively insensitive to changes in ASM and reproductive rates (Eberhardt and Siniff, 1977; Fowler, 1981; Reilly and Barlow, 1986), these parameters have been correlated with changes in population abundance for other marine mammal species (Fowler, 1987). For instance, a decrease in ASM was correlated with a decline in population abundance for baleen whale stocks (Lockyer, 1984). Similarly, a decrease in ASM for crabeater seals was correlated with an increase in the per capita availability of food resources resulting from the exploitation and subsequent reduction in size of baleen whale stocks (Bengtson and Laws, 1985). Likewise, ASM for the striped dolphin of the western Pacific declined in response to exploitation and reduced population abundance (Kasuya, 1985). Based on the predictions of population responses to changes in density (i.e., increases in ASM and decreases in pregnancy rates as population abundance increases) presented by Eberhardt (1977) and Eberhardt and Siniff (1977), we predicted a decline in the ASM for both the northern offshore and southern offshore stocks of spotted dolphin after 1974 as well as a lower ASM for the more heavily exploited northern offshore stock. Similarly, a higher fraction of sexually mature females pregnant and those simultaneously pregnant and lactating should be observed for the northern offshore stock.

Methods

Since 1968, when the National Marine Fisheries Service (NMFS) first placed observers aboard U.S. vessels to observe fishery activities, life history data has been collected from all cetacean species incidentally killed in the ETP yellowfin tuna purse-seine fishery. Beginning in 1974, life history data collection procedures were standardized, and the original sampling scheme that selectively collected large, female specimens was replaced by a random sampling scheme that selected the first available dead dolphins brought aboard (Perrin and Oliver, 1982). In 1979, the Inter-American Tropical Tuna Commission (IATTC) joined the NMFS in placing observers aboard U.S. vessels and collecting life history data.

The offshore stocks of spotted dolphin are distinguished geographically as being north or south of 1° south latitude (Perrin et al., 1985). The specimens used in our study were collected from these areas, but the sample of northern offshore stock animals was additionally restricted to those animals collected west of 120° west latitude (Fig. 1). The northern offshore stock was sub-sampled because exploitation has not been spatially uniform. The yellowfin tuna purse-seine fishery began primarily as a coastal fishery in 1959 and gradually expanded farther offshore. The Commission's Yellowfin tuna Regulatory Area (CYRA) was established in 1968 by the IATTC and provides a useful boundary that separates the inshore fishery area from the westernmost region of the ETP yellowfin tuna fishery (Peterson and Bayliff, 1985). The area west of the CYRA was not fished until the late 1960's, and then only for a few months a year. Exploitation in this region has been significantly less than inside the CYRA but much more than in the southern area which has been fished only sporadically since the early 1970's (Punsly, 1983). Although spotted dolphin move along the 10°N latitude as well as from the south to the west (Perrin et al., 1979a; Au and Perryman, 1985; Reilly, 1990), owing to the large size of the area, interchange between areas is probably limited. A standardized data collection scheme was established at about the same time as the fishery expanded into the western and southern regions of the ETP, and therefore we anticipated that these two distinct geographic regions would provide the best opportunity for testing potential biological indices.

Female spotted dolphins with complete life history data (i.e., geographic position, total body length, teeth collected, and both ovaries examined) collected between 1974 and 1988 were selected for this study. Few specimens have been collected from the southern offshore stock, and therefore all available specimens were prepared. Specimens from the northern offshore stock were selected randomly by year and the sample sizes distributed as evenly as possible between years so that annual estimates of ASM could be calculated. A maximum of 50 specimens per year was the target for selecting specimens from the northern offshore stock sample because Hohn (1989) showed that a sample size of 50 accurately estimated ASM and reduced the variance from an estimate based on a sample size of 25. Thin sections of the teeth were prepared and aged by one of us (ACM) with techniques described in Myrick et al. (1983). Prior to estimating age, all specimens were numerically coded in random order to disguise the specimen number so that no inference could be made about the stock or collection year for any speci-

[1]Smith, T. D. (ed.). 1979. Report of the status of porpoise stocks workshop (August 27–31, 1979, La Jolla, California). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-79-41, 120 p.

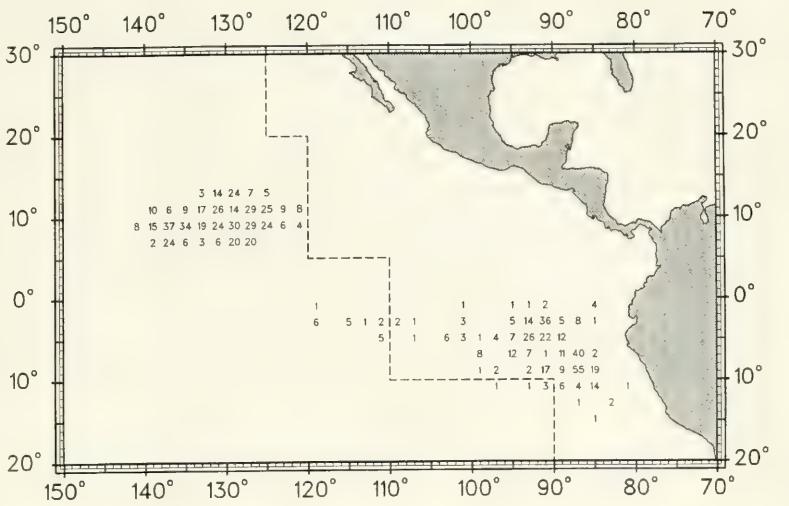

Figure 1

The collection location and sample size of female spotted dolphin specimens selected for this study summarized by 2°-degree square block. The sample of northern offshore spotted dolphins was selected from north of 1° south and west of the Commission's Yellowfin tuna Regulatory Area (the dashed line), and the sample of southern offshore spotted dolphins was selected from south 1° south.

men. The associated life history data were also withheld until each specimen was aged.

ASM and its variance were calculated with the following formula (DeMaster, 1984b; Hohn, 1989).

$$\mathrm{ASM} = x + \sum_{i=x}^{j} p_i$$

$$s^2 = \sum_{i=x}^{j} \{[(p_i * (1-p_i)]/(n_i-1)\},$$

where, x = age of the youngest mature animal,
j = age class of the oldest immature animal,
p_i = proportion immature in age class i,
n_i = sample size for age class i.

Because population abundance estimates are not available for the geographic areas from which our samples were collected, we substituted year as a correlate for evaluating potential biological indices. We tested for temporal trends in ASM with a linear regression to determine whether the slope was statistically significantly different from zero. In addition, data for each stock were pooled for all years, and the null hypothesis of no difference between estimates of ASM for the two stocks was tested with a Student's t-test.

Other reproductive parameters examined include the fraction of the females mature, and the fraction of mature females that were either pregnant or lactating, or simultaneously pregnant and lactating. Trends in these parameters between 1974 and 1988 were tested by using a chi-square test for linear trends (Snedecor and Cochran, 1973), and the mean estimates for each parameter, all years combined, were tested for statistically significant differences with a chi-square test.

Results

Average age at attainment of sexual maturity

ASM was estimated for each year with sufficient data available (Table 1): 1976–1982 and 1984–1988 for the northern offshore stock sample, and 1976, 1979, and 1982 for the southern offshore stock sample. The regression line fit to the data for the northern offshore stock was not statistically significantly different from zero. We did not fit a regression line to the data from the southern offshore stock because only three annual estimates were available. The pooled estimate of ASM for each stock was 11.1 years (SE=0.236; n=520) for

Table 1

Number of samples by year and state of sexual maturity (immature or mature) for the northern offshore and southern offshore stocks of spotted dolphin used to estimate the average age at attainment of sexual maturity.

	Offshore stock			
	Northern		Southern	
Year	Immature	Mature	Immature	Mature
74	0	0	0	0
75	0	0	0	5
76	13	33	41	101
77	16	28	2	6
78	17	27	1	23
79	18	25	16	49
80	15	28	2	9
81	13	24	6	5
82	12	20	42	68
83	9	9	11	11
84	11	27	1	4
85	17	29	0	0
86	18	28	0	0
87	22	26	0	0
88	14	21	0	0
Total	195	325	122	281

the northern offshore spotted dolphin and 9.8 years (SE=0.264; n=403) for the southern offshore spotted dolphin (Fig. 2). This difference in the ASM was statistically significant (t=14.32, df=13, P< 0.001). The range in age of animals attaining sexual maturity was largest for the northern offshore stock. The youngest mature animal was 7 years, and the oldest immature was 16 years. The same range for the southern offshore stock was 6 to 11 years (Fig. 3).

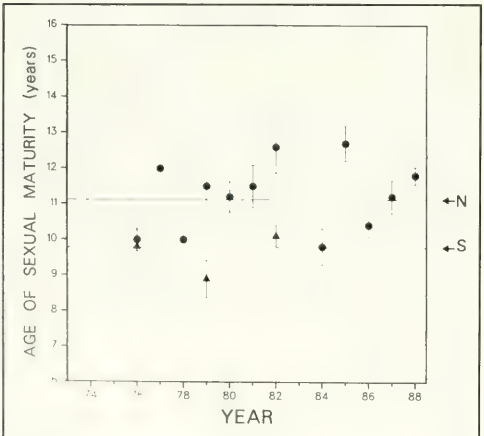

Figure 2

Estimates of the average age at attainment of sexual maturity (ASM) by stock for the offshore spotted dolphin with 1 SE. If no SE bar was plotted, then there were no overlapping indeterminate age classes. Circles represent estimates of ASM for the northern offshore stock and triangles are the estimates for the southern offshore stock. The pooled estimate of ASM for the northern offshore stock (N) is 11.1 years (solid line) and 9.8 years (dashed line) for the southern offshore stock (S).

Reproductive rates

The statistically significant trends in the reproductive parameters examined were an increase in the proportion of mature females simultaneously pregnant and lactating in the northern offshore stock, the predicted compensatory response, and a decrease in the proportion of mature specimens in the sample from the southern offshore stock. When the data for all years were pooled, no statistically significant differences between the mean parameter estimates for the northern offshore and southern offshore stocks were detected (Table 2).

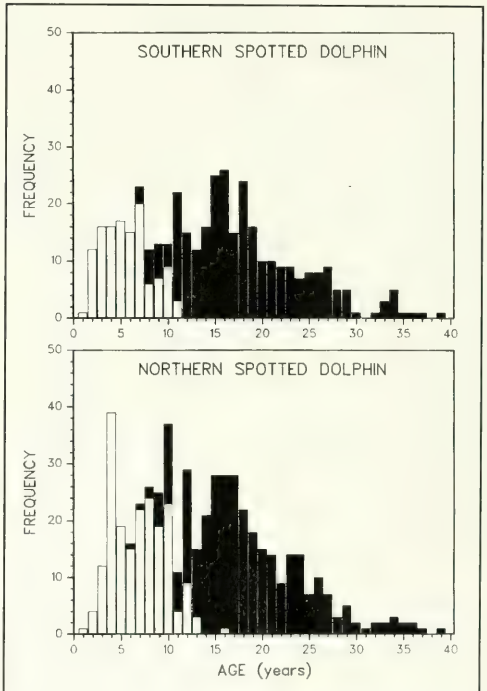

Figure 3

Age-frequency distribution of the northern offshore and southern offshore spotted dolphin specimens aged. The open bars represent the sexually immature females in the sample, and the solid bars represent the sexually mature females in the sample.

Table 2

The mean proportion of females by reproductive condition for the northern offshore and southern offshore stocks of spotted dolphin: the proportion of females in the sample that were sexually mature, and the proportion of sexually mature females that were pregnant or lactating, or simultaneously pregnant and lactating.

Reproductive condition	Stock	
	northern	southern
Mature	0.62	0.69
Pregnant	0.33	0.40
Lactating	0.55	0.47
Pregnant and lactating	0.06	0.06

Discussion

Published evidence of density dependence in dolphin species is rare, and results are inconsistent. For example, in Japan, the striped dolphin, *Stenella coeruleoalba*, is heavily exploited, and the length of the lactation period is reported to have declined (Kasuya and Miyazaki[2]). For exploited spotted dolphins in the western Pacific, a decline in the ASM from 10.1 years in the 1961–63 cohorts to 8.6 years in the 1964–66 cohorts was reported, although the regression coefficient was not statistically significant (Kasuya, 1985). The decline in ASM for female striped dolphin from 9.7 years for the 1956–58 cohorts to 7.4 years in the 1968–70 cohorts was statistically significant (Kasuya, 1985). On the otherhand, for the spinner dolphin (*S. longirostris*) in the ETP, the less exploited southern whitebelly stock has a shorter lactation period than the more heavily exploited eastern spinner dolphin, the opposite of what would be expected for a compensatory response. The annual pregnancy rate, however, is lowest for the southern whitebelly stock and highest for the more heavily exploited eastern stock, as expected for density compensation (Perrin and Henderson, 1984). Barlow (1985) also reported differences in the proportion of mature female spotted dolphins (*S. attenuata*) that were pregnant between the eastern and western Pacific. The lowest proportion of mature females pregnant was observed in the more heavily exploited population, again, contrary to predictions based on the reported exploitation rates and estimates of population abundance for the ETP spotted dolphin. Also, for ETP spotted dolphins, the proportion of lactating mature females significantly increased from 46% in 1973 to 69% in 1981 ($P<0.05$) presumably in response to exploitation; no other statistically significant trends in reproductive parameters were found (Myrick et al., 1986).

Comparisons with other studies are difficult because in most cases the degree of exploitation relative to K has not been quantified, and techniques to estimate age and ASM vary. In our study, statistically significant temporal trends were not detected for ASM but were detected for some of the reproductive parameters. The increase in the proportion of mature females simultaneously pregnant and lactating for the northern offshore stock and the decrease in the proportion of mature females in the population for the southern stock both suggest that the populations are growing. The fact that we did not observe the predicted compensatory responses in ASM may be due to one or more factors, including 1) too few data, 2) parameter estimation or measurement error, 3) a time lag in the response, or 4) biological differences between the stocks. Too few data and environmental periodicity (e.g., El Niño) may increase the variability in annual estimates of parameters, and both factors would reduce the ability to detect differences in potential compensatory responses (Goodman, 1984). The order in which parameters respond to changes in population density is not known, but time lags in responses may be expected owing to the late age at which these animals reach sexually maturity and the multi-year breeding cycle characteristic of the spotted dolphin (Goodman, 1981).

Data for the southern offshore stock of spotted dolphin, in particular, were limited and precluded testing for trends in ASM or the selected reproductive parameters. Although we selected our sample size, a maximum of 50 specimens per year for the northern offshore stock, on the basis of earlier work describing the effect of sample size on the variance for estimates of ASM (Hohn, 1989), our results indicate that larger sample sizes would be required to reduce the variance of the estimates in order to detect small, but biologically significant, changes (e.g., a 1.5-year difference) in ASM. Sample sizes of fewer than 50 per estimate of ASM resulted in too few specimens in the indeterminate age classes (i.e., those age classes with both sexually immature and mature animals) to estimate ASM accurately.

Another concern when analyzing data collected from a kill is whether the age distribution is representative of the population. All immature age classes appear to be underrepresented in both stocks, especially age classes between 10 and 15 years of the northern offshore stock (Fig. 3). This phenomenon was noted in a previous aging study of ETP spotted dolphin but occurred about five age classes earlier than the one we observed (Barlow and Hohn, 1984). This difference may be a result of different readers estimating age,

[2]Kasuya, T., and N. Miyazaki. 1975. The stock of *Stenella coeruleoalba* off the Pacific Coast of Japan. Pap. ACMRR/MM/SC-25 pres. at FAO Scientific Consultation of Marine Mammals, Bergen, February, 1976, 36 p.

although a Kolmogorov-Smirnov test to compare the age-frequency distributions of sexually immature and sexually mature animals from the two studies concluded that the samples were likely drawn from the same population. The underrepresentation of the immature age classes may be a result of segregation in the population by age and sex, fairly typical in large mammal populations, and may affect the estimation of ASM. We investigated the effect of this underrepresentation by assuming a stable age distribution and by apportioning the animals in the indeterminate age classes by sexual maturity under different assumptions of sexual maturity for animals in those age classes, and then calculated ASM. On the basis of segregation by age and sex observed in other species of large mammals, we predicted that the most reasonable scenario for reconstructing the age distribution is that the "missing" animals would be sexually immature. If this indeed were the case, we have underestimated ASM. Under this and other scenarios we investigated, estimates of ASM were consistently over- or under-estimated for both stocks. Therefore, possible sampling biases were unlikely to be responsible for the observed differences in ASM between the northern offshore and southern offshore stocks of spotted dolphin.

The hypotheses we tested required that several implicit assumptions be made, including: 1) constant data collection biases, 2) minimal interchange of animals between areas, 3) consistent estimation of specimen age, 4) linear compensatory response with change in population abundance, 5) constant carrying capacity (K), and 6) equivalent initial life history parameters for the two stocks. The first three of the assumptions are believed to hold reasonably well. Barlow (1985) tested several of the same life history parameters we examined and found them to be relatively insensitive to a number of potential data collection biases; no major changes in the collection of life history data were made after 1974, thus supporting constant data collection bias as a reasonable assumption. Furthermore, the fishery operates in the same areas from year-to-year at approximately the same time of year. In fact, 60% of our sample from the northern offshore stock was collected between July and September, and a further 38% was collected between April and June; in the south, 57% of the sample was collected between January and March, and 27% was collected between October and December. This pattern of sample collection was consistent from year-to-year, and therefore would not affect the pooled or annual estimates of ASM or reproductive parameters. Geographic variability has been noted in earlier studies of spotted dolphin life history data (Hohn and Hammond, 1985; Barlow, 1985); thus selecting specimens from discrete areas as we did reduces the potential for geographic variability to obscure population compensatory responses. Similarly, estimating the age of all specimens at one time and in the blind ensured that age estimates were made as consistently as possible. Information about the validity of assumptions 4) and 5) is not currently available, but violations of the assumptions may provide explanations for our results. There is evidence for differences in the morphological and life history characteristics between the northern offshore and southern offshore stocks of spotted dolphin (see Perrin et al., 1976, 1979b, 1991[3]; Barlow, 1985; Hohn and Hammond, 1985; Myrick et al., 1986; Bright and Chivers[4]) that are likely correlated with the different oceanographic environments of the areas inhabited by these stocks (Au and Perryman, 1985; Reilly, 1990).

We did not find conclusive evidence for compensatory responses in these stocks of spotted dolphin as only one reproductive parameter for each stock showed a statistically significant trend. However, observed trends in both parameters suggest the populations are below K and declining. Our comparison of ASM's suggest further biological differences between the northern offshore and southern offshore stocks or populations. Currently, the order of compensatory responses and their dynamics are not known. In order to be useful as a biological index, a measure of the status of the population must be known and the dynamics of the parameter over a wide range of population densities quantified (Fowler and Siniff, 1992).

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[3]Perrin, W. F., G. D. Schnell, D. J. Hough, J. W. Gilpatrick, and J. V. Kashiwada. 1991. Re-examination of geographical cranial variation in the pantropical spotted dolphin *(Stenella attenuata)* in the eastern Pacific. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-39, 46 p.

[4]Bright, A. M., and S. J. Chivers. 1991. Post-natal growth rates: a comparison of northern and southern stocks of the offshore spotted dolphin. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-30, 24 p.

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PCR-RFLP analysis on thirteen western Atlantic snappers (subfamily Lutjaninae): a simple method for species and stock identification

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Abstract.—Restriction endonuclease analysis of mitochondrial cytochrome *b* and 12S ribosomal RNA (rRNA) gene fragments amplified by polymerase chain reaction (PCR) was applied to thirteen western Atlantic snapper species (the genera *Lutjanus*, *Ocyurus* and *Rhomboplites*), in order to assess reliability of this method for genetic species and stock identification studies. Eight species (*L. apodus*, *L. buccanella*, *L. campechanus*, *L. cyanopterus*, *L. griseus*, *L. synagris*, *L vivanus* and *R. aurorubens*) could be identified by haplotype analysis on either single or both fragments, while the others (*L. analis*, *L. jocu*, *L. mahogoni*, *L. purpureus* and *O. chrysurus*) were not separated from one another because of overlapping or identical haplotypes observed between species. High nucleon diversity estimates (h = 40–80%) observed within four species (*L. campechanus*, *L. cyanopterus*, *L. griseus* and *L. jocu*) indicated that sufficient intraspecific polymorphism could be detected by the PCR-[RFLP] restriction fragment length polymorphism analysis making it a useful method for investigating genetic stock structure.

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In order to manage fisheries resources, it is essential to know the recruitment mechanisms of a given species. Lutjanidae is one of the largest teleostean families, comprising 4 subfamilies, 17 genera, and 103 species (Allen, 1985). More than a half of the lutjanid species belong to the subfamily Lutjaninae in which 14 species under three genera (*Lutjanus*, *Ocyurus* and *Rhomboplites*) have been described in the western Atlantic Ocean. All are fine food fishes and very important for commercial and recreational fisheries, and considerable concern has been focused on the need to understand recruitment in order to manage these reef species (Huntsman, 1981; Doherty, 1983; Roberts and Polunin, 1991). However, the close morphological similarity of larvae among lutjanid species, especially within the subfamily Lutjaninae, has made specific identification of larvae a difficult task (Richards, 1985; Leis, 1987; Richards and Lindeman, 1987). Allozyme electrophoresis has proven useful for identifying some fish species even at their embryonic or larval stages (Morgan, 1975; Smith and Crossland, 1977; Mork et al., 1983; Graves et al., 1989). Since DNA is virtually the same in any cell type of an individual and can be extracted from ethanol-preserved specimens, restriction fragment analyses of DNA is becoming a preferred method to investigate variation and relationships between fish species (Billington and Hebert, 1991). Distinct restriction fragment patterns between three bass species of the genus *Paralabrax* could be detected in ethanol-preserved individual eggs and larvae *via* Southern blot analysis (Graves et al., 1990). Although conventional mitochondrial DNA (mtDNA) methods are powerful for detecting variation in restriction fragment length, intensive DNA analysis would be difficult especially on very small samples, such as fish embryos or larvae, which offer a very small amount of DNA. To overcome this problem, the use of the polymerase chain reaction (PCR) method, which can amplify DNA sequences more than 10-million fold (Saiki et al., 1988), is neccessary. In this paper, we report amplification of two mitochondrial genes (cytochrome *b* and 12S rRNA) using fresh or frozen samples, ethanol-preserved embryos and larvae, and alcohol-preserved museum samples of thirteen western Atlantic snapper species, and results of restriction fragment length polymorphism (RFLP)

analysis on these two DNA fragments within and between species.

Materials and methods

Sample collection

The species used and sources of collection are listed in Table 1. All of the fresh or frozen specimens were collected in the Miami and Key West, FL, area during 1990 and 1991. Fertilized eggs and hatched larvae of *Lutjanus synagris* were raised at 28°C in 380-L tanks and fed a combination of cultured rotifers and wild-caught zooplankton. The eggs (4 to 6 hours after insemination) and larvae (3 and 9 days old) were fixed with 95% ethanol and kept for two months at room temperature. Two eggs and two larvae were randomly chosen. All of the museum specimens were obtained from the Ichthyology Museum at the University of Miami. The time since preservation ranged from 5 to 42 years and it is likely that most were fixed with formaldehyde first and then transferred to ethanol or isopropyl alcohol (C. R. Robins, Professor, Rosenstiel School of Marine and Atmospheric Science, Division of Marine Biology and Fisheries, Univ. Miami, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, pers. commun.). However, exact records on preservation methods were not available. Samples are labelled as to source, for example, Lcy1 and LcyM1 designate *Lutjanus cyanopterus* fresh or frozen specimen No. 1 and *L. cyanopterus* museum specimen No. 1, respectively.

DNA extraction

Fresh or frozen specimens Mitochondria-enriched or total genomic DNA samples were prepared from fresh or frozen specimens by the method of Chapman and Powers (1984) with slight modification.

Museum specimens A piece of white muscle (0.1–0.2 g) was dissected from each individual, shredded and rinsed in TEK buffer (50 mM Tris, 10 mM EDTA,

Table 1

Sample species of snappers (Lutjaniae: *Lutjanus, Ocyurus* and *Rhomboplites*) and source of collection.

Species	Abbreviation	Fresh or frozen samples locality and date	Museum samples label, locality, and date
L. analis	La	Miami, FL, '90,'91 (6)*	
L. apodus	Lap	Miami, FL, '90,'91 (7)	
L. buccanella	Lb	Miami, FL, '91 (4)	
L. campechanus	Lc	NA	UMML 27092, 28°N, 80°W, '66 (M2)**
			UMML 27093, 28°N, 80°W, '66 (M1)
			UMML 27096, 11°N, 60°W, '66 (M3)
			UM/M2422, Gulf of Mexico, '58 (M4-5)
L. cyanopterus	Lcy	Key West, FL, '91 (1)	UMML15923, Virgin Isl., '59 (M1)
			UM/M4868, Bahama, '56 (M2)
L. griseus	Lg	Miami, FL, '90,'91 (9)	
L. jocu	Lj	NA	Cat.No. 1944, Puerto Rico, '57 (M1)
			Cat.No. 620, Cutler, FL, '49 (M2-4)
			UMML34424, Miami, FL, '86 (M6)
			UM/M5660, Miami, FL, '64 (M7)
L. mahogoni	Lm	Key West, FL, '91 (2)	UMML7523, Knight Key, FL, '57 (M1)
			UM/M4865, Miami,FL '50 (M2)
L. purpureus	Lp	NA	UM/M6093, Venezuela, '65 (M1-2)
			St.5708, Venezuela, '65 (M3)
			St.5658, Venezuela, '65 (M4)
			UM/M6086, Venezuela, '65 (M5-6)
L. synagris	Ls	Miami, Key West, FL, '90 (7)	
L. vivanus	Lv	Miami, FL, '90,'91 (5)	STA5739, Panama, '65 (M1)
O. chrysurus	Oc	Miami, Key West, FL, '90 (8)	
R. aurorubens	Ra	Miami, FL, '90 (6)	

NA=not available.
=number of individuals examined
**=museum specimens were labelled, for example, as LcM1 designating *Lutjanus campechanus* museum specimen No. 1. All museum samples were obtained from the Ichthyological Museum of the University of Miami. UMML is the catalogue number for each individual; values in parentheses indicate lots in which several individuals were contained.

1.5% KCl, pH 7.5) for 10 minutes at room temperature. The muscle fibrils were finely minced and homogenized in 5–10 mL of ice-cold TEK buffer by means of a motor-driven, glass-teflon homogenizer. Five or more strokes of the homogenizer were neccessary to grind the toughest muscle tissue. The homogenate was transferred to a plastic centrifuge tube (50-mL capacity), and SDS and proteinase K were added as described in Chapman and Powers (1984). The sample was then incubated at 65°C for 2 hours or more and vigorously shaken at intervals. This crude sample was phenol-chloroform extracted and ethanol precipitated as described in Chapman and Powers (1984). The amount of DNA was usually too small to be seen as a pellet, but was rehydrated in 500 µl of TE buffer (1 mM EDTA, 10 mM Tris-HCl, pH 8.0) and transferred to a 1.5 mL microcentrifuge tube. To concentrate this DNA sample, ethanol precipitation was repeated and the pellet was rehydrated in 10 µl of TE buffer.

Embryos and larvae Each specimen was transferred to a 1.5-mL microcentrifuge tube. TEK buffer was added and decanted several times to rinse specimens and to remove ethanol. The specimen was then homogenized in 500 µl of TEK buffer and total DNA was isolated as described above. The pellet was rehydrated in 10 µl of TE buffer.

Amplification of mitochondrial cytochrome *b* and 12S rRNA genes

The two pairs of primers used that targeted cytochrome *b* and 12S rRNA genes were abbreviated forms of those described by Kocher et al. (1989). The nucleotide sequences of each set of primers were as follows: cytochrome *b*, 5'-GCTTCCATCCAACATCTCAGCATGATG-3' and 5'-GCAGCCCCTCAGAATGATATTTGTCCTC-3'; 12S rRNA, 5'-TCAAACTGGGATTAGATACCCCACTAT-3' and 5'-TGACTGCAGAGGGTGACGGGCGGTGTGT-3'. These primers were synthesized by R. K. Werner in the Department of Biochemistry and Molecular Biology at the University of Miami.

Polymerase chain reaction was carried out in a final volume of 50 µl in a reaction mixture described by Kocher et al. (1989). This reaction mixture was preheated at 94°C for 3 minutes followed by 30–35 cycles of amplification (93°C for 1 min, 44°C for 1 min, and 72°C for 1 min). The same cycle was applied to amplify both cytochrome *b* and 12S rRNA genes. After amplification, the reaction mixture was separated from covering oil and transferred to a 1.5-mL microcentrifuge tube. TE buffer (0.5 mL) was added to the reaction mixture, followed by chloroform: isoamylalcohol (24:1) extraction and ethanol precipitation. After centrifugation at 12,000 × g for 10 minutes, the pellet was dried under reduced vacuum, rehydrated with 10 to 50 µl of TE, and stored at 4°C.

Endonuclease digestion for amplified DNA fragments

Nine restriction endonucleases used were *Alu* I, *Cfo* I, *Dde* I, *Hae* III, *Hin* fI, *Mbo* I, *Msp* I, *Rsa* I, and *Taq* I, all recognizing symmetric 4-base pair sequences. One unit of each enzyme was applied to 1 to 2 µl of amplified PCR product in a final reaction volume of 5 µl. The digested samples were electrophoresed through 2% NuSieve (3:1) (FMC BioProducts, Rockland, ME) agarose gels in TBE buffer (90 mM Tris-boric acid, and 2 mM EDTA). DNA bands were visualized and photographed following electrophoresis and staining with ethidium bromide.

Data analysis The size of fragment amplified and restricted was estimated in comparison with a size standard (1 kb ladder, BRL). Nucleotide sequence divegence (p) (Upholt, 1977) was calculated by using the proportion of shared restriction fragments between specimens. Restriction patterns by each endonuclease were designated A, B or C for composite haplotype analysis, and the number of haplotype was used to estimate nucleon diversity (h) (Nei and Tajima, 1981) within species.

Results

Gene amplification

Each pair of primers successfully amplified 355±5 bp and 450±5 bp fragments of the cytochrome *b* and 12S rRNA genes, respectively. There were no apparent differences in the fragment size among species. Both DNA fragments in all of the fresh and frozen specimens and in ethanol-preserved embryos and larvae were well amplified. In contrast, the amount of DNA was usually much less in museum specimens, to the extent that PCR did not always amplify one or both of the gene fragments.

Restriction fragment analysis

Figure 1, A and B, shows representative restriction patterns with diagnostic enzymes for amplified fragments of the cytochrome *b* and 12S rRNA genes. The restricted fragment distributions for nine enzymes of 72 individuals in cytochrome *b* and 59 individuals in 12S rRNA genes are shown in Tables 2 and 3.

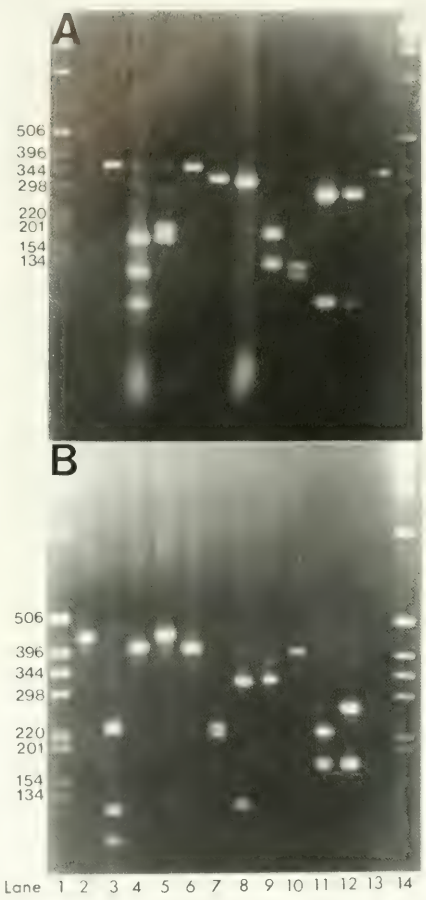

Figure 1

Restriction profiles of cytochrome *b* (**A**) and 12S rRNA (**B**) gene fragments amplified by PCR. (A) lanes 1 and 14 (size standard), 2 (blank), 3 and 4 (La and Ra digested by *Alu* I), 5 and 6 (Lap and Lv digested by *Cfo* I), 7 and 8 (La and Ra digested by *Dde* I), 9 and 10 (Ra and Ls digested by *Hae* III), 11 and 12 (Lap and Ra digested by *Hin* fI), and 13 (La no digestion); (B) lanes 1 and 14 (size standard), 2 (La no digestion), 3 (La digested by *Alu* I), 4 (Lb digested by *Cfo* I), 5 (Ls digested by *Dde* I), 6 (Lg digested by *Hae* III), 7 (Oc digested by *Hin* fI), 8 (Ls digested by *Mbo* I), 9 and 10 (Lg and La2 digested by *Msp* I), 11 and 12 (Lg and La digested by *Taq* I), and 13 (blank).

For the 355 bp cytochrome *b* fragment, four enzymes (*Mbo* I, *Msp* I, *Rsa* I and *Taq* I) had no restriction sites in any of the species. *Dde* I had restriction site(s) in all species examined, without apparent size difference in restricted fragments within and between species. Variation on the restricted fragment length within and between species was observed for four of the nine enzymes examined. *Alu* I appeared to have no restriction sites in this fragment of all *Lutjanus* spp. and *O. chrysurus* (Oc), but two restriction sites producing three fragments (170, 110 and 74 bp) were evident in *R. aurorubens* (Ra). *Cfo* I, *Hae* III and *Hin* fI digestions revealed polymorphism within species; *L. griseus* (Lg) for all three enzymes, *L. analis* (La) for *Cfo* I and *Hin* fI, *L. campechanus* (Lc) for *Hae* III and *Hin* fI, and *O. chrysurus* (Oc) for *Cfo* I only.

All nine enzymes had recognition site(s) in the 450 bp 12S rRNA fragment of at least one species. No length variation of the restricted fragments between species was observed for *Cfo* I and *Hae* III digestions. *Taq* I digestion produced 230 and 170 bp fragments in *L. griseus* (Lg), while 280 and 170 bp fragments were observed in the other species. Intraspecific polymorphism was observed for the other six enzymes; *Alu* I (for Lc, Lcy, Lg, and Lj), *Dde* I (for Lc, Lcy, and Lg), *Hin* fI (for La, Lap, Lcy, and Lj), *Mbo* I (for La, Lc, and Lj), *Msp* I (for La, Lcy, and Lj), and *Rsa* I (for Lc, Lcy, and Lj).

Data of restriction fragment patterns were summarized for haplotype analysis for species discrimination (Table 4). Straightforward diagnostic restriction profiles were observed in the 12S rRNA fragment of *L. griseus* (Lg) digested by *Taq* I and in the cytochrome *b* fragment of *R. aurorubens* (Ra) digested by *Alu* I, without RFLP within species. Haplotype analysis on cytochrome *b* fragment separated *L. cyanopterus* (Lcy) and *L. vivanus* (Lv), and that on 12S rRNA gene fragment separated *L. campechanus* (Lc). *L. apodus* (Lap), *L. buccanella* (Lb) and *L. synagris* (Ls) were descriminated by haplotype analysis on both fragments. In contrast, identical haplotypes were found in five individuals of *L. analis* (La1, 5, 52–54), all of *L. mahogony* (Lm1, 2, M2) and in seven of *O. chrysurus* (Oc1–7), and in two individuals of *L. jocu* (LjM2, M3) and in one of *L. purpureus* (LpM2). One individual of *L. analis* (La2), two of *L. jocu* (LjM1, M7), and one of *O. chrysurus* (Oc50) had their own distinct haplotype.

Mean percent nucleotide sequence divergence (p) within species ranged from 0 to 2.43 with an average of 0.65. The nucleotide sequence divergence for those between species within the genus *Lutjanus* ranged from 0.11 to 3.84 with an average of 1.69, for those between

Table 2

Restriction profiles of 355 bp cytochrome *b* gene fragment of 13 snapper (Lutjanidae) species. 1=present; 0=absent.

		Species and sample number																
		La		Lap	Lb	Lc		Lcy	Lg		Lj	Lm	Lp	Ls	Lv	Oc		Ra
Enzymes and fragments		1,5, 52–54	2	1–7	1–4	M1, M2,M3	M4	1, M1,M2	2–5, 8–10, 13	6	M1–M3	1,2,M2	M1–M6	1–6, 9	1–5, M1	1–7	50	1–6
Alu I	355	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
	170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	74	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cfo I	355	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	0	1
	185	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1	0
	170	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	1	0
Dde I	330	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hae III	190	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	0	1
	120	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	100	1	1	1	0	0	1	0	1	0	0	1	0	1	1	1	1	0
Hin fI	355	1	0	0	0	0	1	0	1	0	1	1	1	1	0	1	1	0
	275	0	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	1
	80	0	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	1
Mbo I	355	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Msp I	355	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Rsa I	355	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Taq I	355	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 3

Restriction profiles of 450 bp 12S rRNA gene fragment of 13 snapper (Lutjanidae) species. 1=present; 0=absent.

		Species and sample number																		
		La		Lap		Lb	Lc		Lcy		Lg		Lj			Lm	Lp	Ls	Lv	Oc	Ra
Enzymes and fragments		1,5, 52–54	2	1–3	7	1–4	M1, M4	M5	1, M1	M2	2,3,5 6,8,9	4	M1	M2, M3	M7	1,2,M2	M2	1–6,9	1–5,M1	1–7,50	1–3
Alu I	450	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
	230	1	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1
	120	1	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1
	100	1	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1
Cfo I	420	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dde I	450	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
	420	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
Hae III	410	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hin fI	450	0	1	1	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	1
	230	1	0	0	1	1	0	0	1	0	1	1	0	1	0	1	1	0	1	1	0
	220	1	0	0	1	1	0	0	1	0	1	1	0	1	0	1	1	0	1	1	0
Mbo I	450	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
	320	1	0	1	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
	130	1	0	1	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Msp I	450	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
	400	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	320	1	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1
Rsa I	450	1	1	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1
	250	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0
	120	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0
Taq I	280	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1
	230	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	170	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4

Haplotypes of 74 individuals of thirteen snapper (Lutjanidae) species, and percent sequence divergence (p) and nucleon divergence (h). Eleven columns represent 9 endonucleases: *Alu* I (1 and 5); *Cfo* I (2); *Dde*I (6); *Hae*III (3); *Hin*fI (4 and 7); *Mbo*I (8); *Msp*I (9); *Rsa*I (10); *Taq*I (11).

Gene	cytochrome *b*				12S rRNA								
specimen	1	2	3	4	5	6	7	8	9	10	11	p*	h**
La1, 5, 52–54	A	A	B	A	B	A	B	B	C	A	B		
La2	A	B	B	B	B	A	A	A	B	A	B	1.2	33.3
Lap1–3	A	B	B	B	B	A	A	B	C	A	B		
Lap4–6	A	B	B	B	—	—	—	—	—	—	—		
Lap7	A	B	B	B	B	A	B	B	C	A	B	0.25	28.6
Lb1–4	A	A	A	B	B	A	B	B	C	A	B	0	0
LcM1	A	A	A	B	B	A	A	B	A	A	B		
LcM2,3	A	A	A	B	not amplified								
LcM4	A	A	B	A	B	A	A	B	A	A	B		
LcM5	not amplified				A	B	A	A	A	B	B	1.54	70.0
Lcy1,M1	A	B	A	B	B	A	B	B	C	A	B		
LcyM2	A	B	A	B	A	B	A	A	A	B	B	2.43	66.7
Lg2,3,5,8,9	A	B	B	A	B	A	A	B	C	A	C		
Lg4	A	B	B	A	A	A	A	B	C	A	C		
Lg6	A	A	A	B	B	A	A	B	C	A	C		
Lg10,13	A	B	B	A	—	—	—	—	—	—	—	0.7	41.7
LjM1	A	A	A	A	A	B	A	A	A	A	B		
LjM2,M3	A	A	A	A	B	A	B	B	C	A	B		
LjM7	not amplified				B	A	A	B	C	B	B	2.18	83.3
Lm1.2,M2	A	A	B	A	B	A	B	B	C	A	B	0	0
LpM1,3–6	A	A	A	A	not amplified								
LpM2	A	A	A	A	B	A	B	B	C	A	B	0	0
Ls1–6,9	A	B	B	A	B	A	A	B	C	A	B	0	0
Lv1–5,M1	A	B	B	B	B	A	B	B	C	A	B	0	0
Oc1–7	A	A	B	A	B	A	B	B	C	A	B		
Oc50	A	B	B	A	B	A	B	B	C	A	B	0.13	25.0
Ra1–3	B	A	A	B	B	A	A	B	C	A	B		
Ra4–6	B	A	A	B	—	—	—	—	—		-	0	0

— = PCR was not attempted.

*Mean percent sequence divergence (Upholt, 1977): individuals possessing incomplete haplotype were excluded.

**Percent nucleon diversity (Nei and Tajima, 1981): individuals possessing an incomplete haplotype were included in the most common haplotype.

Lutjanus and *Ocyurus* ranged from 0.7 to 3.07 with an average of 1.21, for those between *Lutjanus* and *Rhomboplites* it ranged from 1.24 to 2.81 with an average of 2.16, and for that between *Ocyurus* and *Rhomboplites* it was 2.41. Nucleon diversity estimates (h) within species ranged from 0 to 83.3%.

Discussion

Eight out of thirteen western Atlantic snapper species examined may be identified by PCR-RFLP analysis of the two mitochondrial genes, although further analysis for the intraspecific polymorphism is neccessary for

complete discrimination. Snappers are an important component of both the recreational and commercial fisheries in the Southeastern United States, Gulf of Mexico, and Caribbean. Analysis of the distribution of eggs and larvae for life history and recruitment studies of the fishery has been hampered by the inability to identify eggs and larvae of most snapper species. Our results significantly increase the number of eggs and larvae that can be unambiguously identified. Incomplete separation by our methods for all thirteen species is due to sharing of identical haplotypes between some species, which could be caused by possible occurrence of natural hybrids between snapper species (Domeier and Clarke, 1992). The lack of between species resolution may also be attributed to the fact that the amplified fragments are too short for RFLP analysis, since the number of restriction sites is subjected to the fragment length.

Average sequence divergence observed between the snapper species is also low compared with those between congeneric species of other fish taxa where the entire mtDNA molecule was analyzed (see Billington and Hebert, 1991). Bartlett and Davidson (1991) using direct nucleotide sequence of 307 bp cytochrome *b* gene fragment found several distinct nucleotide substitutions between four tuna species of the genus *Thunnus*. Since many of the nucleotide substitutions observed between these tuna species are found to create or destroy palindromic sequences, PCR-RFLP analysis on the 355 bp cytochrome *b* gene fragment alone could identify these tuna species using only a few endonucleases (Chow and Inoue, 1993). They also found that RFLP analysis of cytochrome *b* and 12S rRNA gene fragments provided insufficient variation to separate all eight species of the genus *Thunnus*, but all tuna species could be separated using a 940 bp fragment of flanking region between ATPase and cytochrome oxidase subunit III genes. Similar analysis on the cytochrome *b* gene fragment could separate six billfish Pacific species and five Atlantic species, but separation of all species was incomplete (Chow[1]).

Although it appears that RFLP analysis may fail to pick up distinct nucleotide substitutions between species, analysis on longer fragments may overcome this disadvantage. Thus, differentiation between closely related species appears to vary among regions within the mtDNA and in a given gene may vary among taxa. Recently, Silberman and Walsh (1992) using PCR-RFLP analysis on the 28S ribosomal RNA gene simply and unambiguously distinguished three spiny lobster species of the genus *Panulirus*. Nuclear rDNA may be better suited for species descrimination, where little intraspecific polymorphism is expected (Dover, 1982).

We have observed relatively high intraspecific polymorphism in some snapper species, in which the nucleon diversity (h) of *L. campechanus, L. cyanopterus, L. griseus,* and *L. jocu* are 70, 67, 42, and 83%, respectively. Gyllensten and Wilson (1987), using restriction analysis on the entire mitochondrial DNA molecule, reported nucleon diversity of brown trout (*Salmo trutta*) to be 72%. Carr and Marshall (1991), using direct nucleotide sequence of a 298 bp cytochrome *b* gene, reported that of the western Atlantic and Norwegian populations of Atlantic cod (*Gadus morhua*) to be 36 and 88%, respectively, comparable with those of some snapper species. It is highly probable that some snapper species contain a large number of maternal lineages within the population, which can be detected by PCR-RFLP analyses as demonstrated in this study.

The present study indicates that PCR-RFLP analysis is much simpler and less expensive than conventional mtDNA and nucleotide sequence analyses and better suited for large-scale genetic surveys requiring large numbers of specimens. With this method, not only are quantitative analyses of species composition at early life history stages possible, but also intensive genetic analysis. Since relatively little is known about the spawning habits, dispersal, and migration of these snapper species, it would be very interesting to compare, for example, genetic structures between adults and their early life stages. Such genetic analyses would aid in evaluating the utility of management schemes, such as reserves and protected areas.

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Effects of dolphin group type, percent coverage, and fleet size on estimates of annual dolphin mortality derived from 1987 U.S. tuna-vessel observer data

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Abstract.—Amendments enacted in 1988 to the U.S. Marine Mammal Protection Act of 1972, coupled with changes during the 1980's in the composition of the international purse-seine fleet fishing "on dolphin" for yellowfin tuna in the eastern tropical Pacific (ETP), motivated a simulation experiment to assess the effects of fleet size and observer coverage level on estimates of cumulative annual mortality for dolphin stocks, where data quality differed greatly between stocks. Results from this simulation study provided a basis for subsequent U.S. legislation regarding criteria for comparing dolphin mortality rates of U.S. vs. non-U.S. fleets fishing in the ETP, pursuant to regulations governing import of tuna from this area.

Accuracy and precision of mortality estimates were influenced very strongly by data quality (dolphin group type) and moderately strongly by fleet size and level of observer coverage. Because neither fleet size nor dolphin group type can be controlled by a sampling program, desired levels of accuracy and precision in estimates of dolphin mortality can be achieved only by manipulating the level of observer coverage. The unexpectedly strong effect of dolphin group type implies that to protect all groups equally, observer levels should be chosen to accommodate the dolphin group type exhibiting the poorest-quality data.

U.S.-registered tuna purse-seiners in the eastern tropical Pacific Ocean (ETP) inadvertently kill dolphins during fishing operations (DeMaster et al., 1992). Since 1972 this kill has been monitored by scientific observers accompanying seiners on routine fishing trips. The kill data are monitored to determine whether annual quotas have been reached for dolphin mortality overall, and for several specific stocks of dolphins. If any quota is reached, fishing must cease on the affected stock for the remainder of the calendar year. Since 1989, the data have also been used to determine annual dolphin mortality rates for comparison with non-U.S. fisheries[1].

Prior to 1987, this kill monitoring was accomplished by observers on 30–50% of the trips made by U.S. purse-seiners during a given year. Thus, mortality was estimated rather than measured directly. In the absence of any alternative (i.e., higher rates of observer coverage), the accuracy and precision of these estimates were assumed to be adequate. This assumption was acceptable at the time because the U.S. fleet was large and generated many data. About 100 vessels fished the eastern tropical Pacific Ocean (ETP) each year, each vessel making two to five trips of about three-months duration each.

The situation changed dramatically in the 1980's when, for a variety of reasons (Sakagawa, 1991), the U.S. fleet began to decrease 20–30% per year, decreasing from over 90 vessels in 1981 to about 10 vessels in 1992. This decrease in size of the U.S. fleet was offset by a reciprocal increase in number of non-U.S. vessels fishing in the ETP. This increase has been dominated by Mexican vessels (fleet size exceeding 50 vessels by 1990) but also includes smaller fleets from several other nations. These smaller fleets range in size from 1 to about 20 vessels (IATTC Annual Reports, 1980–1991). In addition to these changes in composition of the international fleet, amendments passed in 1988 to the U.S. Marine Mammal Protection Act stipulated that yellowfin tuna caught in the ETP could be imported from non-U.S. countries only if mortality rates for those countries were comparable to U.S. kill rates.

These events created a strong incentive to evaluate the effects on mortality estimates of varying observer coverage levels and fleet sizes. Because the new regulations pertained to some individual stocks in addition to dolphin mortality overall, the previously uninvestigated effect of dolphin group type was also of interest.

[1] The mortality estimator used in these simulations (kill/day) is not the same estimator used currently (1993) to determine mortality comparability (kill/set). The reasons for this appear in the methods section.

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The U.S. data set for 1987 provided a unique opportunity to investigate these effects. That year, for the first time, observers accompanied nearly 100% of trips by U.S.-registered purse-seiners to the ETP. By subsampling the 1987 data set, various observer levels and fleet sizes could be simulated and their effects on dolphin mortality estimates studied. In the absence of any other available data, these data were taken by NMFS as roughly representative of the international fleet. The simulation results guided subsequent legislation regarding mortality comparability criteria for non-U.S. fleets in the ETP.

Total annual mortality estimates are presented here for three dolphin groups (all stocks combined): spotted dolphin (*Stenella attenuata*); whitebelly spinner dolphin (*Stenella longirostris longirostris*); and common dolphin (*Delphinus delphis*). These three groups represent the range of data types (good, intermediate, and poor in quality) in the 1987 data set, and are generally representative of data types collected every year that may be affected by variable fleet sizes and levels of observer coverage in future fishing years.

Accuracy and precision of the mortality estimates are presented in terms of relative bias and coefficient of variation. Frequency distributions and analytic confidence intervals are examined for underlying patterns in mortality data responsible for generating observed patterns in accuracy and precision.

Methods

Data

During 1987, 34 U.S.-registered purse-seine vessels carrying certificates that permitted fishing "on dolphins" made a total of 134 fishing trips to the eastern tropical Pacific Ocean (ETP). Of these vessels, 33 made 124 trips that were observed by either a National Marine Fisheries (NMFS) or an Inter-American Tropical Tuna Commission (IATTC) technician. These 124 observed trips comprised the entire population of trips for this study. They accounted for 93% of all trips and 96% of all days spent at sea in the ETP by U.S.-registered tuna purse-seiners during 1987. Trips made by individual vessels within fleets were considered replicates and observed trips were assumed to represent unobserved trips accurately. Data consisted of records of date, time, trip number, set number, and kill per set.

Between 4 and 20 vessels carrying observers departed each month during 1987 (Fig. 1). Approximately the same number (although not necessarily the same vessels) of observed vessels (about 30) fished in the ETP during any given month (Fig. 2). Just over half the trips (65/120) lasted about three months. Trip duration ranged from one to six months (Fig. 2). Number of trips incurring mortality of each dolphin group type ranged from 93 (offshore spotted dolphins; Fig. 3) to 12 (common dolphins).

Dolphin mortality data were not stratified geographically, despite the demonstrated efficiency of this stratification scheme (e.g., Hall and Boyer, 1986) because it can be applied only when data sets provide reasonable numbers of reasonably homogeneous data per stratum. Data tend to be so variable for the less frequently killed groups, such as common dolphins, that mortality estimates tend to be very imprecise (and infrequent) even without stratifying data. This is likely to be a problem for all dolphin types for small fleets in every year[2].

Data quality differed between group types in both frequency and extent of kill. Data for offshore spotted dolphins were the "best" in terms of being most plentiful and most evenly distributed between trips collecting data. The frequency distribution of kill per day per trip (i.e., number of dolphins killed per number of days at sea, for a given trip) is relatively smooth (Fig. 3). Most trips killed about 0.5 dolphins per day, a few

[2]At the time this study was conducted (1988–1989), there were no legal requirements for data stratification. Subsequent to this study, the U.S. Congress enacted legislation (Federal Register Notice Vol. 54, #43, Tuesday March 7, 1989; 54 FR9438-9451) requiring stratification of data for annual mortality estimates into three geographic strata and two dolphin groupings (common dolphins, and all other dolphins).

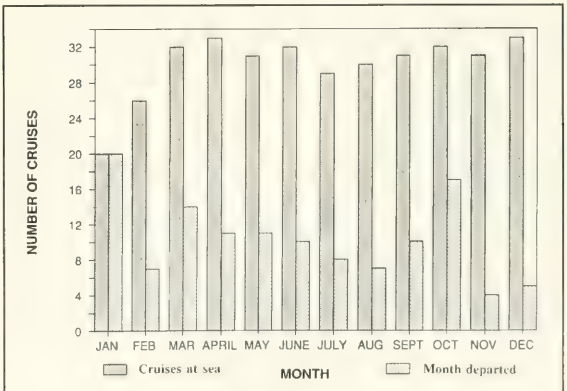

Figure 1
Number of observed U.S.-registered tuna purse-seine vessels at sea, and number of observed vessels leaving port each month during 1987.

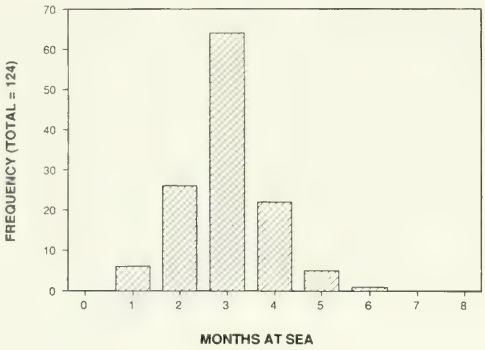

Figure 2
Months spent at sea per trip by U.S.-registered tuna purse-seine vessels carrying observers during 1987.

trips killed no spotted dolphins, and trips with higher kills occurred with decreasing frequency. Data for whitebelly spinner dolphins were intermediate in quality. They were fewer but still relatively smoothly distributed. About half the trips killed no whitebelly spinner dolphins, but of those incurring mortality, most trips were responsible for about 0.1 dolphins per day. Higher kills again occurred with decreasing frequency, with little evidence of extreme outliers. Data for common dolphins exhibited the worst quality, being both sparse and very unevenly distributed. Of the 12 trips incurring mortality of common dolphins, 9 killed about 0.5 dolphins per day, 2 trips killed 1–1.5 dolphins per day, while the remaining trip was responsible for about 9 deaths per day. That one trip was responsible for 67% (594/882) of U.S.-caused common dolphin deaths during 1987.

Simulations

We first selected randomly and without replacement 5, 10, or 20 vessels from the total of 33 observed vessels (Fig. 4). We then sampled randomly and without replacement, 25%, 50%, or 75% of the trips made by each of these selected vessels, without regard to actual timing of those trips throughout the year. We did not force temporal stratification on these small fleet simulations because fleet sizes of 5 or 10 vessels generated so few data.

Vessel selections were replicated 10 times at each combination of fleet size and percent coverage. Trip selections were replicated 50 times from each of the 10 sets of selected vessels. Thus, selected vessels were the same within each set of 50 replicate samples of trips but differed between sets of 50 replicates. Trips conducted by selected vessels in each sample fleet represent the "population" of trips for that fleet replicate.

Each set of 50 replicate selections of trips from a given set of selected vessels generated 50 estimates of cumulative annual mortality (cumulative mortality through December 31). For each set of 50 estimates, we calculated the mean estimate, the coefficient of variation for the mean estimate, and the relative bias of the mean estimate. Thus for each combination of fleet size and percent coverage we generated 10 averaged estimates of annual mortality, 10 coefficients of variation, and 10 estimates of relative bias.

Because the "true" kill varied between fleet replicates depending on the particular vessels and trips selected, the average of these 10 averaged estimates (from the 50 replicates) of annual mortality is not a particularly useful measure in this study. This average represents only the average of the 10 sets of vessels that happened to be chosen for the 10 replicates of fleet size. However, the coefficients of variation and estimates of relative bias for each of the 10 averaged estimates *are* relevant indicators of the ability of the estimation process to precisely or accurately, or both, reflect the true kill, whatever it happens to be for a particular sample of vessels. Accordingly, we present results only for the averages of the 10 estimates of CV and RB generated for each combination of percent coverage, fleet size, and dolphin mortality type. We do not discuss directly the individual mortality estimates.

Estimates

The estimates in this simulation study were derived by using the ratio estimator kill per day, rather than the more precise estimator kill per set (Lo et al., 1982; Hall and Boyer, 1986) because at the time this study was designed and executed, kill per day was still the estimator of choice for NMFS[3].

[3]Kill/day was used by NMFS up until 1987 when 100% observer coverage began, because the quota system required that dolphin kills be monitored continuously throughout the year rather than simply summed at the end of the year. Estimates based on kill/day can be made on a reasonably real-time basis because the day that a vessel leaves port is a readily available datum, and observers report kills by radio on a biweekly basis throughout each observed trip. Number of days fished by the entire fleet (observed plus unobserved) can then be determined relatively simply by summing the number of days at sea since leaving port, and total kill estimated as the product of total fleet days times the estimator kill/day. Biweekly estimates based on kill/set are not possible because observers are not permitted to report set data over the radio. Set data do not become available until after vessels have returned to port.

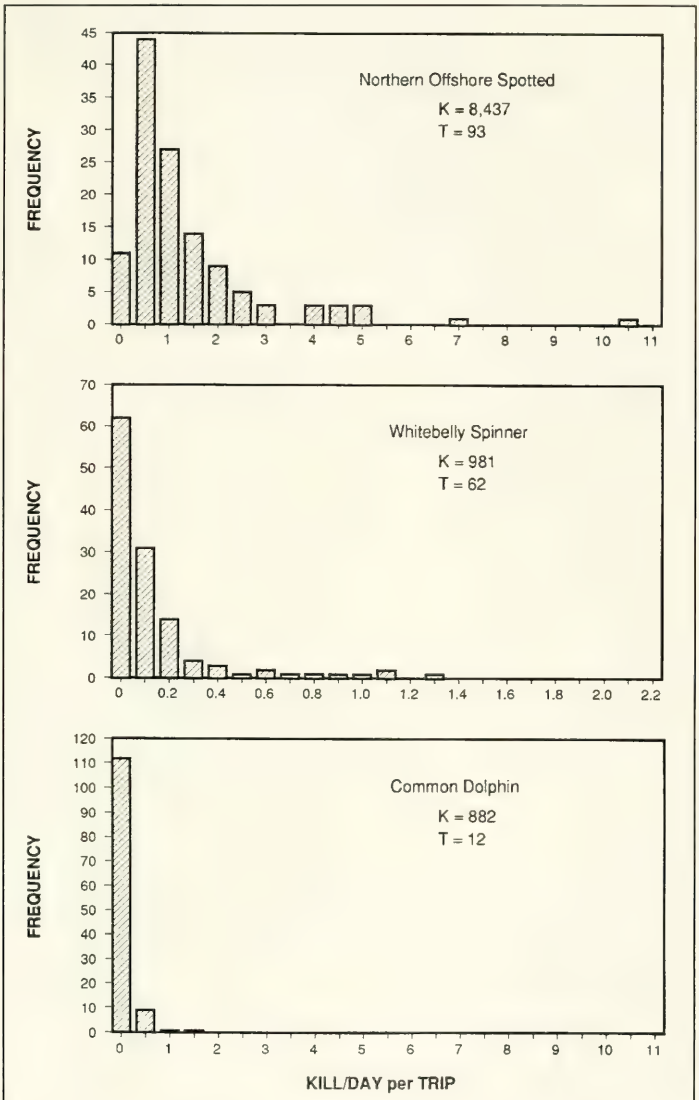

Figure 3

Kill per day during observed trips (124 trips total) by 33 U.S.-registered tuna purse-seiners fishing in the ETP during 1987, for three species of dolphins representing the range of mortality data types. Scales of ordinates and abscissas differ between panels. K is total observed kill during 1987; T is number of trips incurring kill.

Factors and levels included dolphin group$_i$ (i=1,2,3; offshore spotted, whitebelly spinner, and common dolphin), fleet size$_j$ (j = 1,2,3,4; for 5, 10, 20, or 33 boats), fleet replicate$_k$ (k=1,..,10), percent coverage$_l$ (l=1,2,3; for 25%, 50%, and 75%) and percent coverage replicate$_m$ (m=1,...,50).

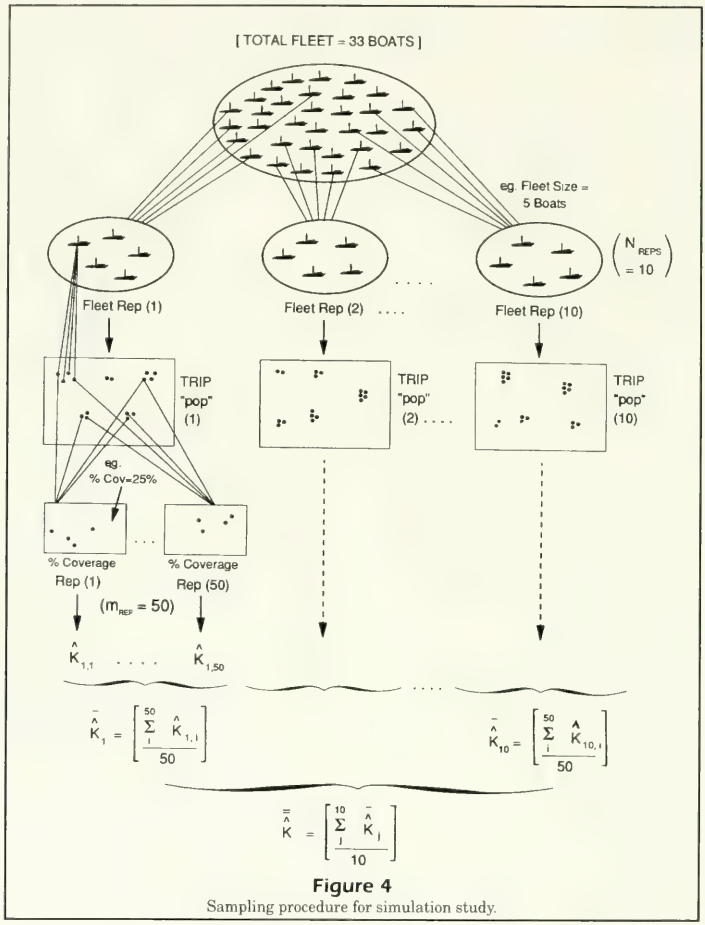

Figure 4
Sampling procedure for simulation study.

Within each replicate, cumulative annual mortality for a given group of dolphins (*YHAT*) is estimated as

$$YHAT_{ijklm} = (K_{ijklm} / DAYS_{jklm}) * TFDAYS_{ijk}$$

where K_{ijklm} is the observed cumulative annual kill on all selected trips, $DAYS_{jklm}$ is the observed number of days, and *TFDAYS* is the total number of days spent at sea by all vessels selected for that replicate.

For each set of 50 replicate estimates of annual mortality for a given fleet size, percent coverage, and dolphin group type, we calculated the average estimate ($YAVE_{50}$), the relative bias of that estimate (RBY_{50}), and the coefficient of variation of that estimate (CVY_{50}) as follows

$$YAVE_{50ijkl} = (1/50) * \sum_{m=1}^{50} YHAT_{ijklm}$$

$$RBY_{50ijkl} = 100 * (YAVE_{50ijkl} - known\ kill_{ijk}) / known\ kill_{ijk}$$

and

$$CVY_{50ijkl} = [\sqrt{MSE(YAVE_{50ijkl})} / known\ kill_{ijk}] * 100$$

where

$$MSE(YAVE_{50ijkl}) = \sum_{m=1}^{50} (YHAT_{ijklm} - known\ kill_{ijk})^2$$

and

$$BYAVE_{50ijkl} = YAVE_{50ijkl} - known\ kill_{ijk},$$

where $BYAVE_{50ijkl}$ is the bias of $YAVE_{50}$, and $V(YAVE_{50ijkl})$ is the variance of $YAVE_{50ijkl}$, calculated as

$$V(YAVE_{50ijkl}) = (1/49) * \sum_{m=1}^{50} (YHAT_{ijklm} - YAVE_{ijkl})^2$$

(Cochran, 1977).

The preceding equations produce 10 $YAVE_{50}$'s, 10 RBY_{50}'s, and 10 CVY_{50}'s for each combination of fleet size, percent coverage, and dolphin group type.

The average of these 10 RBY_{50}'s is

$$RBY_{10ijk} = (1/10) * \sum_{k=1}^{10} (RBY_{50ijkl}),$$

and the average of the 10 CVY_{50}'s is

$$CVY_{10ijk} = (1/10) * \sum_{k=1}^{10} CVY_{50ijkl}.$$

Sampling distributions and confidence intervals

To facilitate interpretation of patterns seen in relative bias and coefficients of variations, we plotted both frequency distributions and analytic 95% confidence intervals for an arbitrarily selected single set of 50 individual replicate estimates of mortality derived under various combinations of conditions. The frequency distributions and confidence intervals illustrate, in particular, variations due to differences between replicates in the fleet selected, in contrast to the relative bias and coefficient of variation, which pertain to sampling properties of the estimator. Only one set of 50 replicates, of the 10 sets generated under each combination of fleet size and coverage level, is illustrated for each combination because the general messages conveyed by the figures were the same for all sets.

Frequency distributions and confidence intervals are plotted only for the cases of 5 and 20 boats at 25% and 75% coverage. Combinations of these values spanned the range of fleet sizes investigated and enabled us to examine whether problems might occur even with coverage as high as 75% when fleet size is as small as 20 (or worse, 5) boats.

The frequency distributions of the 50 estimates illustrate graphically the influence of various combinations of fleet size and observer coverage level on the behavior (dispersion) of the estimator itself (kill/day). The analytic confidence intervals for the 50 estimates illustrate the influence of various combinations of fleet size and observer coverage level, on the estimated precision that may be associated with any individual estimate.

The analytic confidence intervals for individual replicate estimates of mortality were calculated by the International Mathematical and Statistical Library (IMSL) routine SMPRR for ratio estimates (IMSL, 1987). This routine calculates confidence intervals for ratio estimates using the analytic formula for approximate variance of a ratio. The procedure is based on the assumption that a normal approximation to the ratio variance is appropriate (Cochran, 1977; IMSL, 1987). Where data are sparse (fewer than 30 data points in the data set; i.e., in most of the cases in these simulations) this assumption is generally inappropriate (e.g., Cochran, 1977), but for single replicates we had no computationally simple alternative. Bootstrapping confidence intervals for these individual replicates would have eliminated any need for a normal approximation but would have required significantly more computer time to convey essentially the same gross patterns and general message.

Results

Relative bias (RB)

RB was generally small overall, but exceeded the management objective of 5% for common dolphins and whitebelly spinner dolphins when coverage was low (25%; Fig. 5).

Coefficients of variation (CV)

CV decreased with increasing percent coverage and with increasing fleet size in both the "best" data group (offshore spotted dolphin; Fig. 6) and in the "intermediate" data group (whitebelly spinner dolphin). CV decreased with increasing percent coverage but showed no consistent effect of fleet size in the "worst" data group (common dolphin).

Sampling distributions

Frequency distributions were affected somewhat by fleet size (primarily by shifting the central tendency), noticeably by percent coverage (primarily by decreasing the spread of the distribution), and very strongly by dolphin group type (primarily in terms of the number of modes in the distributions; Figs. 7, 8, and 9). Bias and variability increased with small sample sizes and non-smooth data distributions.

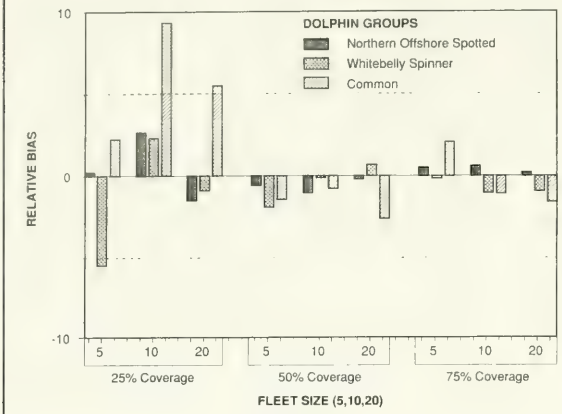

Figure 5

Average relative bias (%) in estimates of annual dolphin mortality as a function of fleet size and percent observer coverage. Dashed line at +5% and –5% indicates management target.

Distributions of mortality estimates for offshore spotted dolphins tended to be relatively narrow and unimodal for fleets of both 5 and 20 vessels, at high coverage (75%; Fig. 7). Distributions remained unimodel but were more dispersed, at low coverage (25%). Distributions for whitebelly spinner dolphins were also unimodal in general but tended to be more dispersed than was the case for offshore spotted dolphins (Fig. 8). Distributions for common dolphins were markedly bimodal and dispersed under all sampling conditions, reflecting the selection (or not) of the one trip with unusually high kill (Fig. 9).

Modal values of mortality estimates for all three dolphin types increased with increasing fleet size (not surprisingly, because more boats generally kill more dolphins) regardless of coverage level. Dispersion also increased with fleet size, more obviously when observer coverage was low than when coverage was high, as more data became available for analysis.

Confidence limits

Confidence limits were affected similarly to frequency distributions. Limits were affected most strongly by dolphin group type, very noticeably by percent coverage, and less strongly but still noticeably by fleet size (Figs. 10, 11, and 12).

Mortality estimates were most stable and confidence intervals dramatically reduced for offshore spotted dolphins at high (75%) observer coverage (Fig. 10). Mortality estimates were more variable and confidence intervals wide and ragged, even with a relatively large fleet (20 boats), for offshore spotted dolphins at low observer coverage (5%). Intervals were most unstable at the combination of lowest observer coverage and smallest fleet size[4]. Confidence interval patterns for whitebelly spinner dolphins were intermediate, being more variable than patterns for northern offshore spotted dophins but being less variable than patterns for common dolphins (Fig. 11). At low coverage and small fleet size, confidence intervals for whitebelly spinner dophins showed the same bimodality characteristic of confidence intervals for common dolphins under all conditions. At high coverage, confidence intervals showed the same relatively stable and

[4]The irregular pattern of the confidence intervals observed for mortality estimates from small fleets (e.g., 5 boats) with low coverage (e.g., 5 boats, 25% coverage) are not surprising because this combination of fleet size and percent coverage means that the mortality estimates are being derived from about 4 observed trips during an entire year (assuming 5 boats make 3 trips/year, 15 trips × 0.25 = 4 trips).

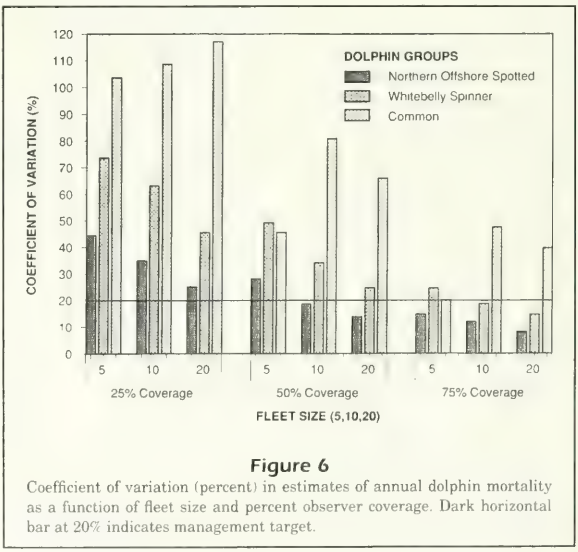

Figure 6

Coefficient of variation (percent) in estimates of annual dolphin mortality as a function of fleet size and percent observer coverage. Dark horizontal bar at 20% indicates management target.

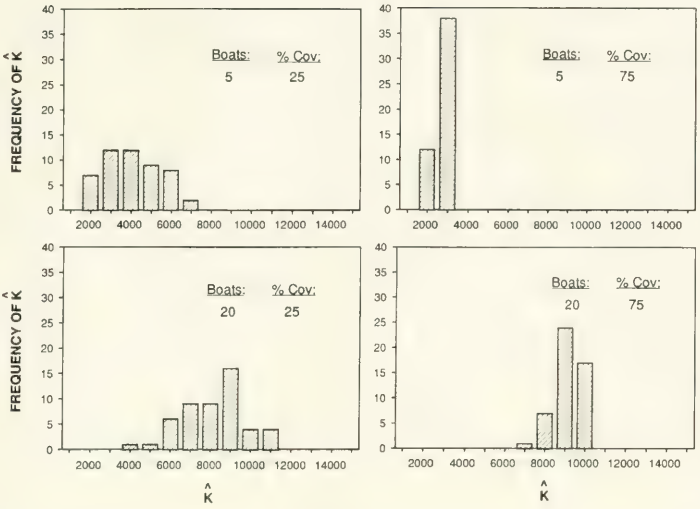

Figure 7

Effect of percent coverage and fleet size on frequency distributions of annual mortality estimates for **offshore spotted dolphins**, from one set of 50 replicates.

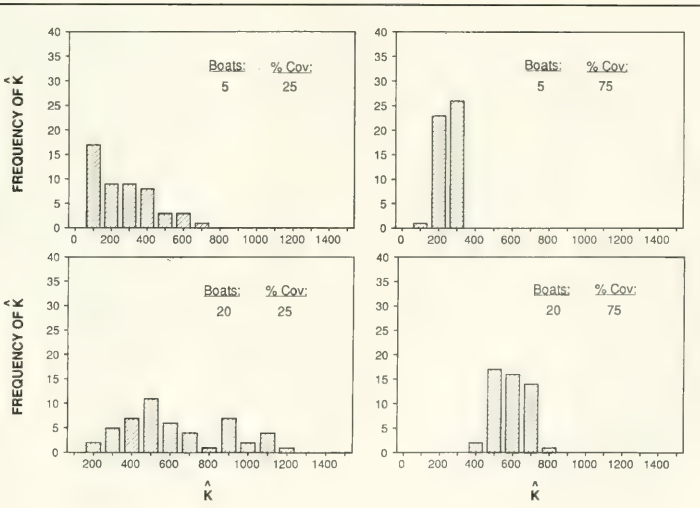

Figure 8

Effect of percent coverage and fleet size on frequency distributions of annual mortality estimates for **whitebelly spinner dolphins**, from one set of 50 replicates.

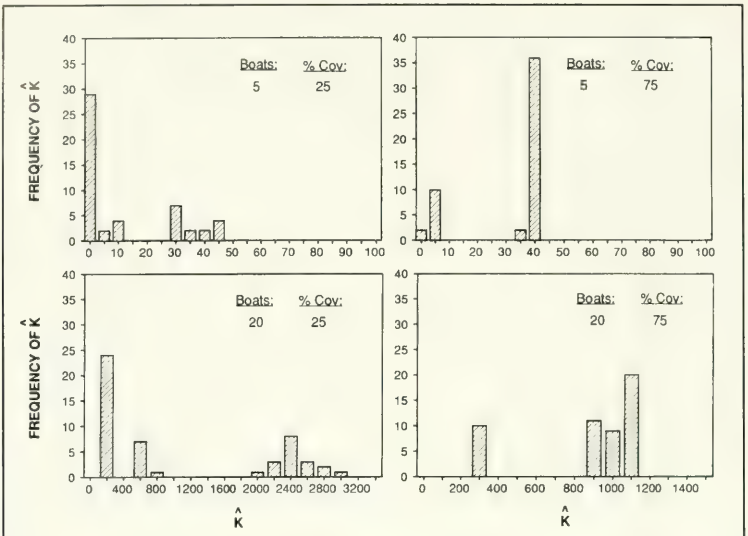

Figure 9

Effect of percent coverage and fleet size on frequency distributions of annual mortality estimates for **common dolphins**, from one set of 50 replicates.

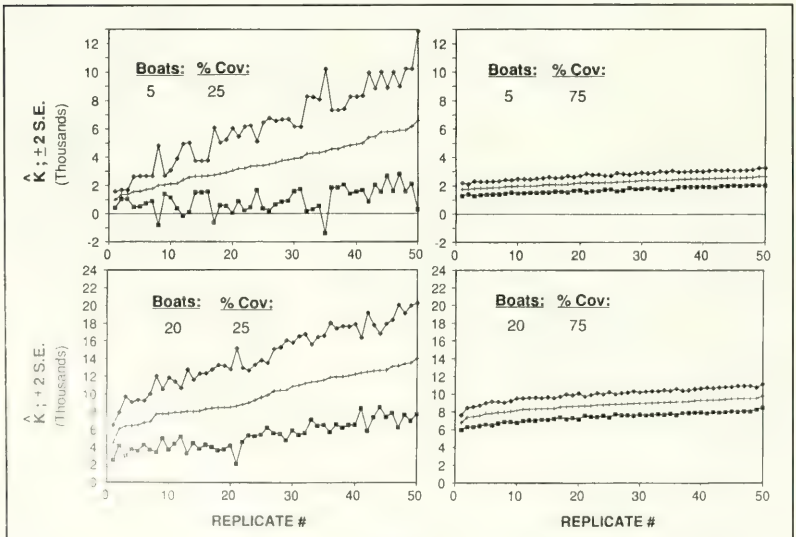

Figure 10

Effect of percent coverage and fleet size on analytic confidence intervals of replicate annual mortality estimates for **offshore spotted dolphins**. Replicate estimates sorted by estimate level, from one set of 50 replicates. Note differences between panels in Y scale.

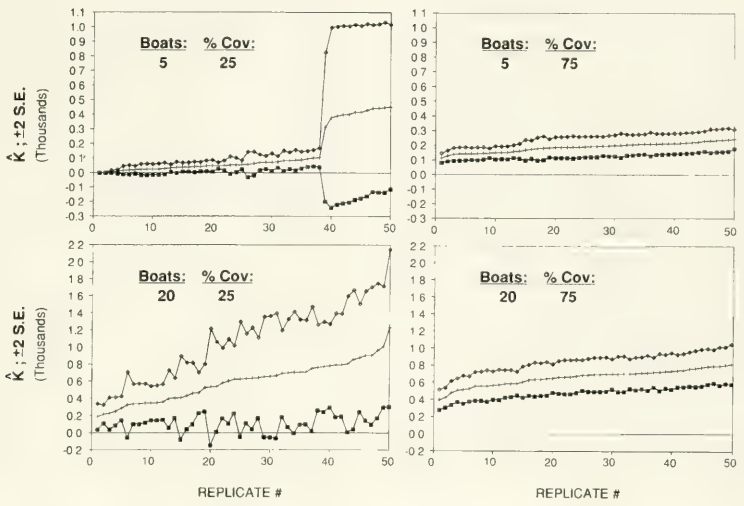

Figure 11

Effect of percent coverage and fleet size on analytic confidence intervals of replicate annual mortality estimates for **whitebelly spinner dolphins**. Replicate estimates sorted by estimate level, from one set of 50 replicates. Mortality estimates expressed in thousands. Note differences between panels in Y scale.

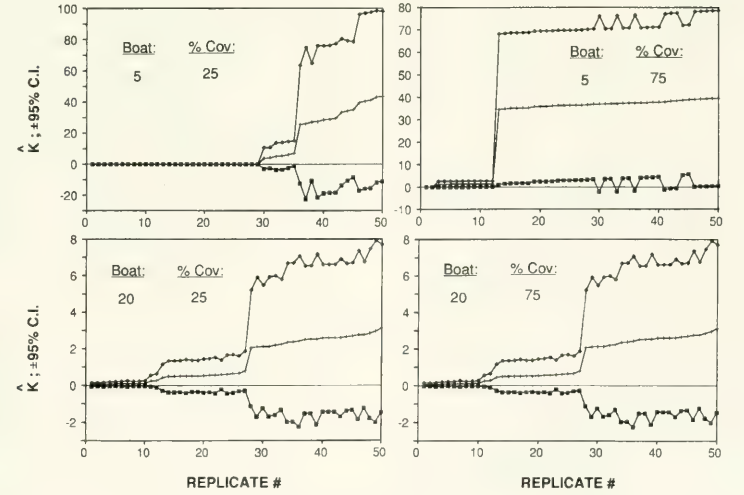

Figure 12

Effect of percent coverage and fleet size on analytic confidence intervals of replicate annual mortality estimates for **common dolphins**. Replicate estimates sorted by estimate level, from one set of 50 replicates. Mortality estimates expressed in thousands. Note differences between panels in Y scale.

narrow limits seen for offshore northern spotted dolphins at high coverage. Confidence intervals for common dolphins illustrate the problems inherent in relatively heterogeneous data, where mortality is sometimes quite high, usually relatively low, and data overall are relatively few. For this species, confidence intervals were extremely variable even with relatively high coverage (Fig. 12) and were very narrow (or nonexistent) for replicates which fortuitously included only low-kill data, but very wide for replicates including a few very high kills.

Although these analytic confidence intervals are clearly inappropriate measures for precise estimation of variance characteristics of the estimates (note negative intervals in some cases; Figs. 10, 11, and 12), they are presented here because they provide an effective illustration of the effects of varying conditions on the variability of the mortality estimates. Despite the inter-group differences, the general response to increasing coverage and increasing fleet size is similar in all three dolphin group types. Confidence intervals become narrower and more stable as more data become available.

Discussion

Dolphin group type

Of the three factors investigated here (dolphin group type, observer coverage level, and fleet size), dolphin group type had the greatest effect on dolphin mortality estimates, followed by percent coverage and fleet size. This hierarchy of effects is controlled by two characteristics of the kill data for each dolphin group type—*frequency* (the number of times that mortality occurs) and *variability* (differences between times in the number of dolphins killed). The *total* number killed can have relatively little influence on the quality of the estimate. This is illustrated by comparing results for whitebelly spinner dolphin and common dolphin. Although total kill was comparable for both dolphin group types (981 deaths of whitebelly spinner dolphin, 882 deaths of common dolphin; Fig. 3) the data sets differed markedly both in number of trips incurring kill (62 for whitebelly spinner dolphin, 12 for common dolphin) and in the distribution of kill per day among those trips (Fig. 3).

The data set for common dolphins exhibits the worst of both characteristics; frequency of kill was low (few trips killed common dolphins) and variability between trips in kill per day was high. These problems exemplify an unfortunate interaction between data collection problems and the ecology of the dolphins themselves. Mortality of common dolphins due to the U.S. fleet during 1987 was *infrequent* because the geographic range of this species is relatively limited and occurs primarily within Mexico's Exclusive Economic Zone. U.S. vessels rarely fish in this area, therefore common dolphins rarely die in U.S. tuna nets in this area. Mortality was *variable* at least in part because common dolphins have an unfortunate habit (in this context) of forming very large schools, pre-disposing them to the possibility of very large-kill "disaster" sets.

The data set for whitebelly spinner dolphin exhibits a problem with only one of the characteristics; data are relatively infrequent. Unlike the case for common dolphins, kill per day was not extremely variable. This similarity in kill per day generates statistics for whitebelly spinner dolphin that are much less biased and variable than for common dolphin.

Observer coverage level

The effect of observer coverage level is influenced both by fleet size and dolphin group type. To achieve a desired level of precision and accuracy in mortality estimates, observer coverage levels will have to be higher in smaller fleets because the available data will be fewer, and higher in dolphin groups with "messy" data, because observer coverage levels affect the probability of encountering an unusually large kill[5].

Observer coverage will need to be relatively high even for large fleets, when estimating mortality of dolphins with sparse and heterogeneous data. For example, with kill data as sparse and variable as was the case for common dolphins in 1987, nearly 100% coverage would be required to generate CV's lower than 20% regardless of fleet size (Fig. 6). With more frequent and less variable kill data, such as for northern spotted dolphin in 1987, CV's lower than 20% can be achieved with 50% coverage of 10-boat fleets (Fig. 6). When fleet size drops to 5 boats, even this relatively well-behaved data set requires coverage at about 75% to achieve CV's less than about 20%. With coverage as low as 25%, even a fleet size of 20 boats was insufficient to meet the management objective of 20% CV.

Fleet size

In smaller fleets, each data point comprises a larger fraction of the available mortality data. In particular, the influence of unusually large mortalities (e.g., the

[5]The possibility of high kills is more important than the possibility of low kills; this is because all dolphin group types experience zero kill frequently (therefore it is not unusual or unexpected). Also, zero kill is a definitive lower bound, while the upper bound on kill is limited only by the potential school size of the dolphin group.

one trip responsible for over 500 deaths of common dolphins) will be much greater in smaller fleets.

The accuracy and precision of mortality estimates are affected less by fleet size *per se* than by observer coverage level for a given fleet size, and the fleet's variability in kill per day. Kill per day is affected not only by the fishermen's choices of fishing methods and areas, but also by the type of dolphin found associated with a given school of tuna. Because these are not factors that can be controlled, small fleets will generally require higher coverage level than larger fleets to achieve a given level of accuracy and precision in mortality estimates.

Simulation procedures and estimates

The simulation procedure used in this study was designed to reflect the sampling process as it would occur in the real world. More precise and less biased estimates of mortality rates for the population of trips contained in the 1987 data set would have resulted from simple random sampling of the 124 trips in the data set as a whole. But simple random sampling implicitly assumes that all vessels are equal in fishing ability. This is not the case, and it is likely that some fleets as a whole may have greater (e.g., those newer to purse-seining and therefore less experienced) or lesser (e.g,, the more experienced fleets) mortality rates than the average for the ETP purse-seine fleet overall. In addition, in the real world, not all trips made by all purse-seine vessels fishing in the ETP would be available for sampling. Only trips made by the vessels in a particular fleet would be available for sampling, and only those vessels actually observed would contribute data. If vessels (or more properly, the crew) differ in their ability to release dolphins unharmed (or not), then fleets with more (or fewer) "low kill" vessels will have lower (or higher) mortality rates than other fleets of comparable size. Although it would have been possible to estimate the number of trips that would have been made, on average, by a fleet of a given size, and to have then randomly sampled that many trips from the 1987 data base, the results would have been unrealistically precise. The cluster sampling resulting from the selection of trips only after selecting vessels adds variability in the estimates but is more realistic than simple random sampling. The sampling scheme used here is a single stage cluster sampling, for which a ratio estimator is the most appropriate choice of estimation procedure (Cochran, 1977).

Discussion

Although the kill-per-day estimator used in this simulation study is no longer used by NMFS because 100% observer coverage has made estimation unnecessary, the results of this study have general implications for current estimation procedures based on kill per set (e.g., Hall and Boyer, 1986) and for mortality estimation procedures in general where data quality may vary between stocks.

The uneven structure of the data set for common dolphins has unfortunate implications for deriving estimates of mortality for dolphin groups that are characterized by having such infrequent and widely variable kill per day. Specifically, estimates of mortality can vary widely depending on which trips happen to be chosen. In our simulation, we could resample the total population of vessels repeatedly, thus generating relatively unbiased, though individually variable, estimates of mortality. In the real world, only one sample (one set of mortality data per dolphin group type) will be collected per year. If this sample is collected under low percent coverage, it appears very likely that the data may be affected by undetectable sampling biases. This bias is more likely to underestimate than to overestimate mortality because sets with large kill are rare and likely to be underestimated, even though the mortality during such sets may be responsible for a disproportionately large percentage of the total kill.

The problem with missing the rare large-kill sets is that the kill in these sets can apparently be one or two orders of magnitude greater than the "usual" kill. For very abundant groups, missing a few large kills will miss only a small percentage of the total number of dolphins in the group; underestimating mortality could be relatively harmless. For less abundant groups, the large kills might represent a significant proportion of the existing stock. Underestimating this mortality could lead to seriously underestimating the impact of mortality due to fishing operations on these stocks.

In the case of the 1987 data set for dolphin kill by the U.S. fleet, coverage greater than 96% (the highest observed) would be required for all boats in order to generate mortality estimates for common dolphin with CV's less than 20%. Alternatively, if only the most abundant groups are considered (e.g., offshore spotted dolphin), CV's less than 20% could be achieved with only 50% coverage of fleets as small as 5 boats. There appears to be no unique solution that is optimal for all groups.

In addition, the poor quality of the data presented here for common dolphin in fact underestimates the true extent of the problem for this species. In actual practice, the species is managed as three separate stocks rather than as one combined stock as presented here. The data are thus extremely sparse for the individual stocks, and the problems with estimating mortality, given anything less than full observer coverage, are greatly exacerbated.

The results of these simulations, in particular the results for five-boat fleets, and common dolphins, strongly influenced subsequent regulations related to comparability criteria for import of tuna caught by non-U.S. fleets. These regulations now require that mortality data for common dolphins be stratified separately from all other stocks, and that non-U.S. fleets meet the U.S. requirement for 100% observer coverage[6].

Of the three factors discussed here (dolphin group type, percent coverage, and fleet size), only percent coverage can be controlled by the sampling program. Our results imply that providing maximum protection for all dolphin groups would require mandating coverage to achieve a desired level of statistical precision for the dolphin group type with the least statistically stable data.

Acknowledgments

The U.S. fleet simulation study was designed by Bruce Wahlen. Nancy Lo and Peter Perkins provided insightful advice about sampling procedures and statistical methods. We thank also the participants in the Workshop on Estimating Dolphin Mortality, and two anonymous reviewers, who provided many useful comments during the review process.

[6]U.S. regulations for acceptable levels of observer coverage for non-U.S. fleets have progressed from a requirement for 33% coverage of trips made by fleets with 10 or more vessels, 50% of trips on fleets of 5–9 vessels, and 100% of fleets with 1–4 vessels during 1989 and 1990 (Federal Register 12/19/89;Vol. 54 #242, p. 51918–51923), to 75% of all trips regardless of fleet size during 1991 and 1992 (10/18/90; 55 FR 42235 and 10/8/91; 56 FR 50672), to the current requirement for 100% coverage regardless of fleet size (Federal Register 1/8/92; Vol. 57, #8, p. 668).

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Method and precision in estimation of dolphin school size with vertical aerial photography

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Abstract.—Field and laboratory procedures were used to acquire dolphin school size estimates from vertical aerial photographs. Multiple photographs were taken of 48 separate schools during a 1989 eastern tropical Pacific (ETP) dolphin abundance survey. During a 12-week "counting period," three readers did independent counts of dolphins in the photographs. For each school, the best photograph imagery was selected and the mean of the three independent counts was used to estimate its "true" size. The coefficient of variation (CV) for school size estimates (between-reader precision) averaged 5.4% and ranged between 1.2% and 14.6%. Most (92%) of the schools were estimated with precision, resulting in a CV of less than 9.0%. Within-reader CV averaged 3.5% and ranged 1.4%–7.1%, indicating that readers were quite precise. To test if reader methods were constant during the counting period, temporal trends in estimates were tested by linear regression analyses and a repeated-counts experiment with repeated measures analysis of variance (RM-ANOVA). Regression analyses indicated no significant temporal trends or bias in the deviation of counts from the means. The RM-ANOVA showed a significant "reader with time" interaction which was attributed to the relatively high variability between readers in counts made at the start of the experiment. Results suggested that methods were constant and counts were precise after an initial "warm-up" counting session.

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Visual estimation of the number of dolphins in a school is difficult because dolphins dive and the entire school is rarely visible at the sea surface at one time. Shipboard observer estimates can be highly variable and they may be biased (Scott et al., 1985; Anganuzzi and Buckland, 1989). Consequently, estimates of dolphin population abundance derived from visual survey data may be biased, and resulting management decisions aimed at conserving these populations may be inappropriate.

The Southwest Fisheries Science Center (SWFSC) has been conducting surveys to monitor temporal trends in the abundance of eastern tropical Pacific (ETP) populations of the pantropical spotted dolphin (*Stenella attenuata*), spinner dolphin (*S. longirostris*), striped dolphin (*S. coeruleoalba*) and common dolphin (*Delphinus delphis*). These surveys are one part of a multifaceted effort to conserve ETP dolphins subjected to incidental mortality in the international purse-seine fishery for yellowfin tuna, *Thunnus albacares* (Perrin, 1975; Wade and Gerrodette, 1992). Starting in 1987, in response to the problem of potential bias in visual school-size estimates, annual ETP surveys were complemented with aerial photography of dolphin schools. This allowed shipboard-observer estimates to be compared with estimates (of the same schools) taken from counts of dolphins in the photographs.

School size estimates derived from large-format (126-mm) aerial photographs were validated during a 1979 study when five separate schools (size range: 161–396 dolphins) were photographed and then captured in a tuna purse-seine net (Scott et al., 1985). Results showed that dolphin counts from the photographs were not statistically different from counts tallied by hand as dolphins were being released from the net. This suggested that counts from aerial photographs approximated "true" school size.

This report details photographic and counting methods used to derive dolphin[1] school size estimates from large-format vertical aerial photographs. Many of the techniques originated with Scott et al. (1985). The techniques were modified to support the photography and laboratory efforts associated with large-scale ETP dolphin population surveys (i.e., annual surveys of 120 days; covering a 19-million-km^2 study area). After a survey in 1989, three readers did independent dolphin counts from approximately 200 dolphin school photographs (multiple photographs were taken for 48 separate schools) over 12 consecutive weeks. For each school, the best photograph imagery was selected (according to criteria described below) and the mean of the three independent counts was used to estimate its true size. The coefficient of variation (CV) was used to characterize the precision (between-

[1]For purposes of this paper, "dolphin" refers to dolphins as well as small toothed-whales that are included in the photograph sample.

and within-reader) associated with the school size estimates.

One concern was that during the 12-week "counting period," readers might be inconsistent in the application of criteria (cognitive or physical methods, or both) used for counting. If readers were inconsistent, then this might affect the accuracy and precision of the estimates. A two-step approach was taken to address this concern. First, temporal trends in the deviation of counts from the means (see Sokal and Rohlf, 1981, p. 50) were evaluated by linear regression. This approach assumed that the mean of three reader counts was close to the true school size and that the sample error was normally distributed. If individual reader counts were not normally distributed, then this might indicate reader bias or a change in criteria. Second, readers did repeated-counts (at four time points during the counting period) of a known sample of photographed schools. This was done to evaluate the consistency of individual readers (within-reader precision) and to test the hypothesis that dolphin counts (from the same photographs) done at the beginning, middle, and end of the counting period were independent of temporal effects. If the hypothesis proved true, then this would support the idea that counting criteria were constant throughout the counting period.

Materials and methods

At sea

Aerial photographs analyzed in this report were taken with Chicago Aerial Industries KA-62 aerial cameras mounted vertically on a Hughes 500-D helicopter. The helicopter was stationed aboard the National Oceanic and Atmospheric Administration (NOAA) survey ship *David Starr Jordan*. All cameras had forward-motion compensation (to minimize photo image blur from aircraft movement) and a 76.2-mm lens. Large-format (126-mm) Kodak Aerochrome MS 2448 color film was used. In order to minimize the behavioral response (scattering and deep diving) of the dolphin schools to the helicopter, photographs were taken at 244 m (800 ft) altitude. The scale of the photographs at this altitude was 1:3200, the sea surface area in a photograph frame was 366 m^2, and a 2-m dolphin measured 0.63 mm on the film. The camera cycle rate was programmed to expose for approximately 80% film image overlap, i.e., 80% of the area photographed in one frame was photographed again in the next successive frame. Successive exposed photograph frames for a school were recorded as a complete "photo-pass." To enhance the probability of photographing an entire school, multiple photo-passes (avg.=5) were made over a school.

In the laboratory

Counts Light tables equipped with dissection microscopes (0.7× to 7× variable objective and 10× wide-field oculars) were used to view and count the dolphin images during counting. Dolphins were counted by hand-tally while being plotted with a permanent marker on a clear acetate overlay. The marked overlay, when moved to the image overlap area of adjacent frames and aligned over dolphins that were previously plotted, made it easier to identify those dolphins not yet counted in the photo-pass. The photo-pass was the unit on which school size estimates were based (Scott et al, 1985); each pass was counted independently by three readers.

Criteria for selecting the "true" school size For each of the 48 photographed schools, the readers chose (by group consensus) the one photo-pass where the mean of the reader counts was the best estimate of true school size. This decision was based on the precision of the three replicate counts and the reader assigned "quality ratings" for the photo-pass. Ratings reflected how confident the reader was in the accuracy of the count. For each photo-pass, readers independently assigned quality ratings ranging from 1 to 4. A rating of "1" indicated that a photo-pass had "excellent" quality. A rating of "2" indicated that the count was "good" despite the presence of some questionable images (i.e., it was difficult to discern and count dolphins accurately when images were partially obscured by light-glare or when photographic resolution was reduced for deep swimming dolphins because of loss of light with sea depth). A photo-pass was rated "3" or "fair" when more questionable images were encountered, but readers still believed the count was a close approximation of true school size. A photo-pass rated "4" was deemed unusable for size estimation because the reader felt there were too many questionable images and the count was not a reliable estimate of true school size.

One source of between-reader variation in dolphin photograph counts was reader error, where dolphins were missed or counted twice. Variation also occurred because readers differed in their interpretations of whether questionable images were dolphins or merely background water turbulence in the photographs. Based on the premise that "precision leads to accuracy" (Sokal and Rohlf, 1981), for each photo-pass, the CV of the three independent counts was used to monitor the reliability of the school size estimate. For photo-passes where the CV of the counts exceeded 10%, the dolphin school was re-counted (independently) to see if the precision of the estimate could be improved. If the CV was above 15% after a second count, the photo-pass was excluded from the study because the counts

were considered too variable and little confidence was placed in the accuracy of the estimate.

Analytical methods The CV was plotted against the variables "school size" and "quality rating" to evaluate how different school sizes and photograph image qualities affected precision. The CV was also used to characterize the precision of individual readers in repeated-counts as described below.

The percent deviation (PD) is a measure of how distant (+ or −) a count is from the mean. Because this difference is expressed as a percentage of the mean, the PD is a consistent index of deviation relative to changes in the mean. For the PD, let x_{ij} be the ith reader's determination of the size of school j. The average determination (or mean) over three readers of the size of the jth school was given by

$$\bar{x}_j = \frac{1}{3}\sum_{i=1}^{3} x_{ij} \quad . \tag{1}$$

The PD of x_{ij} is expressed as

$$PD_{ij} = \frac{x_{ij} - \bar{x}_j}{\bar{x}_j} * 100 \quad . \tag{2}$$

PD values were plotted to evaluate whether individual reader counts were normally distributed or readers were biased (i.e., tended to count high or low relative to the mean). To test for temporal trends in individual reader counts, PD values were regressed against the variable "time." Time represented the chronological sequence, unique for each reader, in which the 48 schools were counted. Logistically, it was impractical for readers to follow the same sequence in working with the photo-passes.

For the repeated-counts experiment, a known sample of six photographed dolphin schools (henceforth referred to as the "experiment schools"), which varied in school size and image quality, were counted four times. Counts were done once at the start of the counting period, then again every 25 days during the period. Changes with time (temporal trends) due to the variables of "school size," "image quality," and "reader" were tested by using a repeated measures analysis of variance (RM-ANOVA) model from Winer (1971; p. 337).[2] Outlier counts were identified by using Shapiro-Wilk's test for normality at $\alpha = 0.05$ (Shapiro and Wilk, 1965). After log-transformation, data met F-test requirements of homoscedasticity according to Levene's test at $\alpha = 0.05$ (computer program BMDP7D used, Dixon et al. 1988). The RM-ANOVA was computed using the software program SuperANOVA (Abacus Concepts, 1990).

Results and discussion

Scott et al. (1985) reported that dolphin school size estimates derived from aerial photographs were accurate and more precise than visual estimates. They found the standard deviation of estimates (log-transformed) averaged 6% of school size for photographic estimates and 10%–30% of school size for visual estimates. The CV for estimates (untransformed) of the 11 schools used in their precision analysis averaged 8.4% (range: 3.7%–15.1%) indicating slightly less precision when compared with estimates presented here (avg. CV: 5.4%; range: 1.2%–14.6%; Table 1). The difference is explained, in part, by their statistical model, which accounted for variance due not only to independent repetitive counts (2 to 4 per photo-pass), but also due to camera types (126- and 229-mm formats) and multiple photo-passes (2 to 7) for a given school. In the present study, variability was minimized by use of one type of camera (126-mm format) and by including only counts of the single best photo-pass for a school.

School size estimates averaged 146 and ranged between 4 and 633 (Table 1). Most schools (92%) were estimated with precision that resulted in a CV of less than 9.0%, and precision varied little with school size (Fig. 1 and Table 2). Estimate precision tended to decrease with decreased quality of the dolphin school photographs (Fig. 2). PD values (listed in Table 1) plotted for individual readers appeared normally distributed, indicating no between-reader bias in counts of the dolphin images.

Repeated-count data are presented in Table 3. Outlier values for experiment school number III (Table 3) resulted from reader error when dolphins were missed as the marked acetate was moved from the dolphin low density area of the photo-pass (in this case, the beginning of the photo-pass) to the high density area. Alternatively, when dolphins in the high density area were counted first, the precision of the estimate was improved because the majority of dolphins in the school were plotted and counted at the onset; this made it easier to track individual dolphins on adjoining frames.

Within-reader CV for repeated counts averaged 3.5%. Reader 2, the most experienced reader, was most precise in repeated counts (avg. CV: 2.6%; range: 1.4–3.8%) followed by reader 3 (avg. CV: 3.4%, range: 1.5–5.1%), and Reader 1 (avg. CV: 4.7%, range: 2.5–7.1%). The RM-ANOVA showed significant differences between

[2]Model detailed in: Gilpatrick, J. W. Jr. (1992). Using vertical aerial photographs to estimate dolphin school sizes: precision and consistency. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-92-35, 20 p.

Table 1

Counts, mean school size, CV, average quality ratings, and PD values for schools photographed in the 1989 ETP dolphin population survey.

School no.	Species codes[1]	Reader counts[2]			Mean school size	CV (%)	Avg. quality rating[3]	Reader PD[4]		
		R1	R2	R3				R1	R2	R3
1	S.COE	37	35	39	37.0	5.4	1.3	0.0	−5.4	+5.4
2	S.ATT	250	227	221	232.7	6.6	2.7	+7.5	−2.4	−5.0
3	S.LON	153	139	147	146.3	4.8	1.0	+4.6	−5.0	+0.5
4	S.COE	57	54	56	55.7	2.7	2.3	+2.4	−2.9	+0.6
5	S.ATT/S.LON	124	127	130	127.0	2.4	2.3	−2.4	0.0	+2.4
6	S.ATT/S.LON	192	196	216	201.3	6.4	1.7	−4.6	−2.7	+7.3
7	S.ATT/S.LON	274	236	242	250.7	8.2	1.0	+9.3	−5.9	−3.5
8	S.COE	48	47	49	48.0	2.1	1.0	0.0	−2.1	+2.1
9	F.ATT	17	18	18	17.7	3.3	1.0	−3.8	+1.9	+1.9
10	S.ATT/S.LON	81	78	77	78.7	2.7	1.0	+2.9	−0.9	−2.1
11	S.ATT/S.LON	412	416	398	408.7	2.3	1.3	+0.8	+1.8	−2.6
12	S.ATT/S.LON	101	106	118	108.3	8.1	2.3	−6.8	−2.2	+8.9
13	S.LON	20	20	21	20.3	2.8	2.7	−1.6	−1.7	+3.3
14	S.ATT/S.LON	107	113	113	111.0	3.1	1.3	−3.6	+1.8	+1.8
15	S.ATT	118	124	109	117.0	6.5	1.3	+0.9	+5.9	−6.8
16	S.ATT/S.LON	618	607	675	633.3	5.8	2.0	−2.4	−4.2	+6.6
17	P.ELE	400	391	399	396.7	1.2	1.0	+0.8	−1.4	+0.6
18	S.COE	58	53	60	57.0	6.3	1.3	+1.8	−7.0	+5.3
19	S.COE	52	55	61	56.0	8.2	1.7	−7.1	−1.8	+8.9
20	D.DEL	317	323	326	322.0	1.4	1.0	−1.6	+0.3	+1.2
21	D.DEL	326	312	367	335.0	8.5	1.3	−2.7	−6.9	+9.6
22	S.COE	24	23	25	24.0	4.2	1.3	0.0	−4.2	+4.2
23	G.MAC	19	18	19	18.7	3.1	1.0	+1.8	−3.6	+1.8
24	S.COE	75	77	68	73.3	6.4	2.0	+2.3	+5.0	−7.3
25	S.COE	34	30	32	32.0	6.3	1.3	+6.3	−6.3	0.0
26	S.COE	166	171	181	172.7	4.4	1.7	−3.9	−0.9	+4.8
27	D.DEL	66	64	60	63.3	4.8	1.7	+4.2	+1.1	−5.3
28	S.ATT/S.LON	216	216	233	221.7	4.4	1.3	−2.6	−2.6	+5.1
29	S.ATT	25	24	23	24.0	4.2	1.0	+4.2	0.0	−4.2
30	G.GRI	56	64	55	58.3	8.5	1.3	−4.0	+9.7	−5.7
31	S.BRE	4	4	5	4.3	13.3	2.0	−7.7	−7.7	+15.4
32	S.LON	576	678	548	600.7	11.4	2.3	−4.1	+12.9	−8.8
33	S.ATT	38	50	49	45.7	14.6	2.7	−16.8	+9.5	+7.3
34	S.COE	40	39	40	39.7	1.5	1.0	+0.8	−1.7	+0.8
35	S.ATT	88	90	80	86.0	6.2	1.7	+2.3	+4.7	−6.7
36	S.LON	315	324	350	329.7	5.5	1.3	−4.5	−1.7	+6.2
37	S.COE	26	25	24	25.0	4.0	2.0	+4.0	0.0	−4.0
38	S.COE	150	147	156	151.0	3.0	2.0	−0.7	−2.7	+3.3
39	S.BRE	36	34	35	35.0	2.9	1.0	+2.9	−2.9	0.0
40	S.ATT/T.TRU	284	293	337	304.7	9.3	2.3	−6.8	−3.8	+10.6
41	G.GRI	20	19	18	19.0	5.3	1.0	+5.3	0.0	−5.3
42	S.COE	35	34	35	34.7	1.7	1.0	+1.0	−1.9	+1.0
43	S.COE	73	74	88	78.3	10.7	2.0	−6.8	−5.5	+12.3
44	S.COE	154	154	144	150.7	3.8	1.3	+2.2	+2.2	−4.4
45	D.DEL	450	526	474	483.3	8.0	1.3	−6.9	+8.8	−1.9
46	S.COE	80	87	92	86.3	7.0	1.7	−7.3	+0.8	+6.6
47	S.COE	23	24	23	23.3	2.5	1.3	−1.4	+2.9	−1.3
48	S.COE	39	39	37	38.3	3.0	2.0	+1.7	+1.7	−3.7
Average:		145.5	145.9	147.4	145.5	5.4	1.6			

[1]Species codes: S.COE = *Stenella coeruleoalba*; S.ATT = *S. attenuata*; S.LON = *S. longirostris*; F.ATT = *Feresa attenuata*; P.ELE = *Peponocephala electra*; G.MAC = *Globicephala macrorhynchus*; D.DEL = *Delphinus delphis*; G.GRI = *Grampus griseus*; S.BRE = *Steno bredanensis*; T.TRU = *Tursiops truncatus*. Multiple species codes indicate mixed-species schools.

[2]Reader codes: R1 = Reader 1; R2 = Reader 2; R3 = Reader 3.

[3]Obtained by averaging the three independent reader assigned quality ratings.

[4]PD = percent deviation of reader count from the mean.

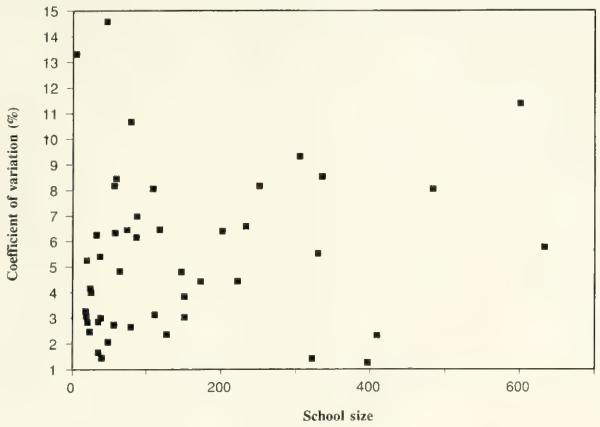

Figure 1

Comparison of mean school size and precision (using CV) of count estimates for schools (n=48) photographed during the 1989 ETP dolphin population survey.

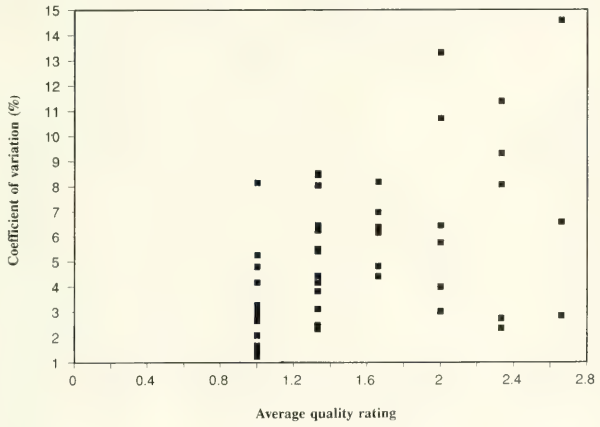

Figure 2

Relationship between photograph quality ratings (averaged for three independent readers) and precision (using CV) of count estimates for schools (n=48) photographed during the 1989 ETP dolphin population survey.

Table 2

Comparison of precision of estimates for small (<125 dolphins), medium (125–350 dolphins), and large (>350 dolphins) schools.

	CV (%)	
School size	Mean	Range
Small	5.3	(1.5–14.6)
Medium	5.2	(1.4–9.3)
Large	5.7	(1.2–11.4)
overall mean:	5.4	
overall range:		(1.2–14.6)

levels of the factors "school size" and "quality rating" (see between-factors; Table 4). This was expected because photographed schools of different sizes were intentionally selected for the analysis. Often, with RM-ANOVA, between-factor effects are confounded with different levels of the factors (as is true for the two factors above) and it is the temporal trends of the within-factor data that are of primary interest in the analysis (Winer, 1971, p. 299). There were no differences between readers in the overall means of their repeated counts (temporal trends not considered; P=0.7898; Table 4).

The F value for the within factor "Time" indicated no significant linear trend for repeated-counts (with the mean of the three reader counts). However, a significant interaction for "reader with time" (F=3.503; P=0.0258; df=6, 31) indicated there were differences between readers in the respective temporal trends of their repeated-counts (Fig. 3). To investigate the source of the significant effect, the trend data for each reader were tested *a posteriori* by contrasts among means with linear coefficients to weigh the log-transformed data (Sokal and Rohlf, 1981; Abacus Concepts, 1990). Results showed the mean of Reader 1's counts at time one differed significantly from the means of counts made at times two, three, and four (F=14.977; P=0.0005; df=1). This suggested that Reader 1's counts made at time one were important in causing the significant "reader with time" interaction.

Because the initial counts (at time one) of the experiment schools were done just prior to the start of the 12-week counting period, this suggested that

Table 3

Repeated counts experiment. Counts of the experiment schools were done at the start of the 12-week counting period, then repeated every 25 days during the period. Observations in parentheses are outlier values.

Schools	School size	Quality rating	Reader	Time			
				Time 1	Time 2	Time 3	Time 4
I	Small	Excellent	1	64	64	66	67
			2	69	66	68	70
			3	61	65	64	69
II	Small	Good	1	34	38	38	35
			2	36	35	36	36
			3	38	39	39	38
III	Medium	Excellent	1	(191)	242	230	236
			2	232	252	236	243
			3	(189)	(193)	(205)	(206)
IV	Medium	Good	1	(169)	214	194	203
			2	207	211	209	206
			3	213	195	194	205
V	Large	Excellent	1	401	468	468	450
			2	457	450	429	432
			3	440	451	429	467
VI	Large	Excellent	1	464	516	525	490
			2	541	527	534	496
			3	507	519	534	527

Table 4

Results from repeated measures analysis of variance (RM-ANOVA).

	df	Sum of squares	Mean square	*F*-value	*P*-value	G.-G.[1] *P*-value
School size	2	8.880	4.4400000	431.485	0.0001	
Quality rating	1	0.290	0.2900000	28.145	0.0003	
Reader	2	0.005	0.0020000	0.241	0.7898	
Error (between factors)	11	0.113	0.0100000			
Time	3	0.002	0.0010000	2.504	0.0775	0.0855
Time * school size	6	0.002	0.0003323	1.653	0.1661	0.2365
Time * quality rating	3	0.001	0.0003299	1.641	0.2001	0.1883
Time * reader	6	0.004	0.0010000	3.503	0.0092	0.0258
Error (within factors)	31	0.006	0.0002011			

[1]*P*-value corresponding to degrees of freedom adjustment using the Greenhouse-Geisser (1959) epsilon factor (=0.692) to correct for correlation of repeated measures. See Anderson (1958); Barcikowski and Robey (1984); Dunn and Clark (1987).

between-reader variance may have been atypically high early in the counting period as well. The regression analyses of PD values with time, however, did not provide strong evidence for this because reader counts were close to the mean values and no significant temporal trends were detected (Fig. 4). Probable cause for the significant effect was that readers were "out of practice" at the start, especially Reader 1. Prior to the

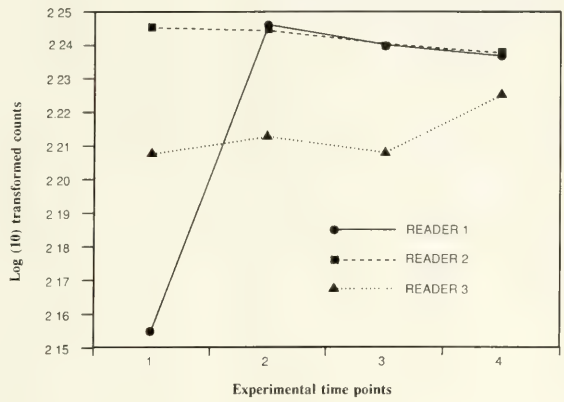

Figure 3

Temporal profiles of the means for counts (log-transformed) made by three independent readers during the repeated-counts experiment.

1991 counting period, a "warm-up" counting session was effective in improving estimate precision, i.e, between-reader CV went from an average of 8% to 4% within one day.

Conclusion

Results suggest that after a prolonged absence from interpreting dolphin school photographs and doing counts, a warm-up session, where readers are refreshed in counting technique, is important for minimizing reader error and improving precision. Estimate precision is also improved when plotting and counting is initiated at the dolphin high-density area in a photopass. The field and laboratory methods described in this report proved reliable in providing precise dolphin school-size estimates for population abundance studies. The CV statistic and PD index will be used for inter- and intra-annual quality control of dolphin school estimates taken from aerial photographs. The analytical methods used in this paper to describe precision and consistency are applicable to other fisheries and terrestrial wildlife research efforts where independent repetitive counts are conducted for parameter estimation.

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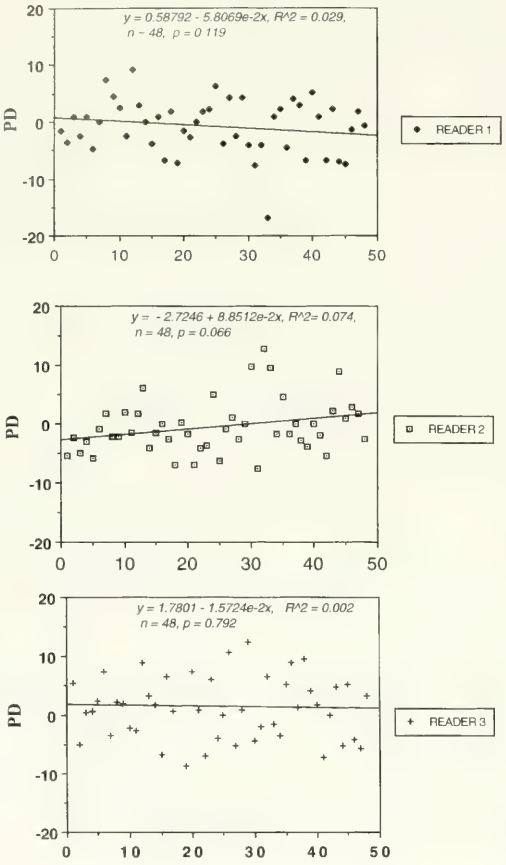

Figure 4

Percent deviation (PD) values regressed on "time." Time represented the chronological sequence, unique for each reader, in which photographed schools were counted during the counting period. Zero on the y axis represents the mean count while negative and positive values represent the percent deviation of the count from the mean.

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Abstract.—Length-frequency data, vertebral-ring-counts, and length measurements of tagged fish were analyzed to independently estimate von Bertalanffy growth parameters for south Pacific albacore (*Thunnus alalunga*). As a working hypothesis, we assumed that the length-frequency modes and vertebral-rings are annual features. The MULTIFAN model fitted to length-frequency data provided estimates of L_∞ and K of 97.1 cm and 0.239 year^{-1}, respectively. Nine age classes were detected in the data. Growth varied seasonally: growth rate decreased to almost zero during August and peaked during February. Two to thirteen rings were visible in the vertebrae, and estimates of L_∞ and K of 121.0 cm and 0.134 year^{-1}, respectively, were obtained. No significant differences in growth parameters were detected between males and females. The growth rates predicted by the length-frequency and vertebral-ring-count models were very similar throughout the range of presumed age classes present in both data sets. These growth rates were consistent with length increment observations from 28 tag returns, which lends support to our assumptions of annual vertebral-rings and length-frequency modes.

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Determination of age and growth of South Pacific albacore *(Thunnus alalunga)* using three methodologies

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Albacore (*Thunnus alalunga*) have been fished in the south Pacific by Japanese longliners since 1952, and by Korean and Taiwanese longliners since 1958 and 1963, respectively (Wang, 1988). Japanese longliners ceased targeting albacore in the mid-1960's, but longline fishing for albacore by Korean and Taiwanese fleets has continued. Since 1960, annual longline catches have fluctuated between 25,000 metric tons (t) and 40,000 t (Anonymous, 1991). In the 1980's, a surface fishery for juvenile albacore developed, comprising drift gillnet vessels from Japan and Taiwan and troll vessels mainly from the United States, New Zealand, Fiji, and French Polynesia. By 1989, the annual surface-fishery catches of albacore had reached about 30,000 t (Anonymous, 1991). The rapid expansion of the surface fishery catalyzed concerns over potential overfishing and possible effects on longline catch rates of larger albacore. This in turn highlighted the need for detailed information on the fisheries and on the dynamics of the albacore population.

Investigations of albacore biology have been conducted since 1985 by scientists from the United States, France, New Zealand, and the South Pacific Commission. The goal of this research has been to obtain information on a range of biological and fishery-related processes, including growth, catch age structure, stock structure, and mortality. Albacore catch rates and size composition in the troll and drift gillnet fisheries have been monitored through a fishery observer program since 1988 (Hampton et al., 1989, 1991; Sharples et al., 1991; Labelle, 1993a). Albacore tagging programs were established in 1986 to provide information on movement, mortality, growth and approximate stock boundaries (Anon., 1986; Pianet et al., 1990; Labelle, 1993b). Catch sampling at major landing sites has been carried out to monitor catch size composition, to collect logbook data, and to obtain samples of bony structures and gonads for estimation of growth rates and spawning periodicity. Estimates of growth rates, and, in particular,

estimates of von Bertalanffy (VB) growth parameters, are important because they are necessary elements in the population dynamic models used in stock assessment.

We used three independent data sets to estimate albacore growth rates: length-frequencies, vertebral-ring-counts, and tag release-recapture statistics. Estimates of VB growth parameters were derived from the length-frequency and vertebral-ring-count data. In both cases, we assumed that the length-frequency modes represent year classes and the vertebral-rings represent annual features. This assumption was tested by using the length increment data from the tag returns.

Materials and methods

Collection of length-frequencies

Length-frequency data were collected by observers from seasonal surface fishery catches between December 1986 and May 1991. All albacore measured were caught by troll vessels on the principal fishing grounds for juvenile albacore, namely the Tasman Sea, along the central east coast of New Zealand, and near the Subtropical Convergence Zone (STCZ), mainly within the area bounded by 35–42°S and 130–170°W (Fig. 1). Throughout each fishing season (typically extending from December to April), observers sampled as many albacore as possible from the daily catches. Albacore were selected at random (i.e., unsystematically), placed on a graduated board, and measured from the tip of the snout (with the mouth closed) to the end of the median caudal ray. These fork-length measurements were rounded down to the nearest centimeter and recorded with the sampling date and fishing location. Tagged albacore were measured in an identical fashion and were combined with the length-frequency samples when it was appropriate.

Most of the length-frequency sampling occurred during 1988–1991 in the STCZ, where catch rates and fishing activity were greatest (Labelle, 1993a). In this region, over 100,000 albacore were measured; sufficient numbers were obtained to stratify samples by month for December–April each season. The number of measurements per month ranged from 351 to 18,908. These data were compiled into length-frequency histograms (Fig. 2), from which VB growth parameters were estimated by using the MULTIFAN computer program (Fournier et al., 1990).

Vertebra collection and processing

Caudal vertebrae were collected during the austral summers of 1986 and 1987 from albacore caught by research vessels trolling in the STCZ, the Tasman Sea, and over the Chatham Rise east of New Zealand (Fig. 1). Vertebrae were also collected during the austral winters of 1987, 1988, and 1989 from albacore caught by Japanese longline vessels fishing off the north east coast of New Zealand near East Cape

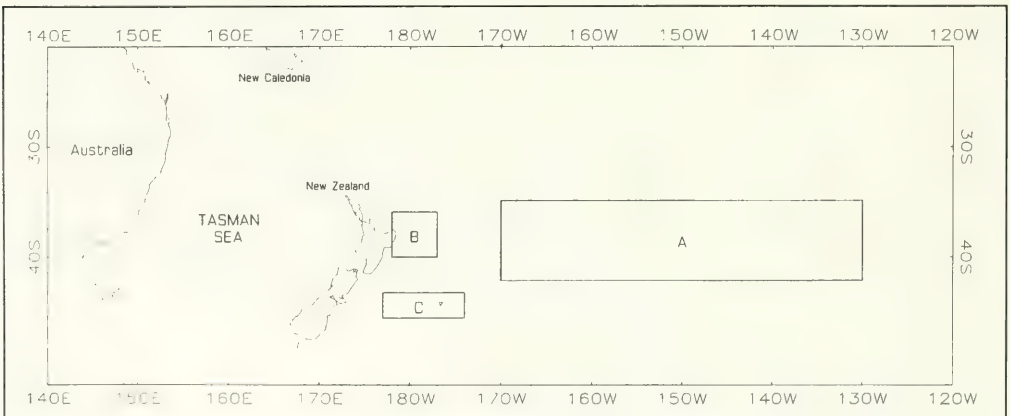


Figure 1

Sampling locations for the collection of length-frequency measurements and vertebrae. Region A covers the main troll fishing grounds centered over the STCZ. Region B delineates the longline fishing area adjacent to East Cape. Region C delineates the Chatham Ridge area where troll fishing occurs.

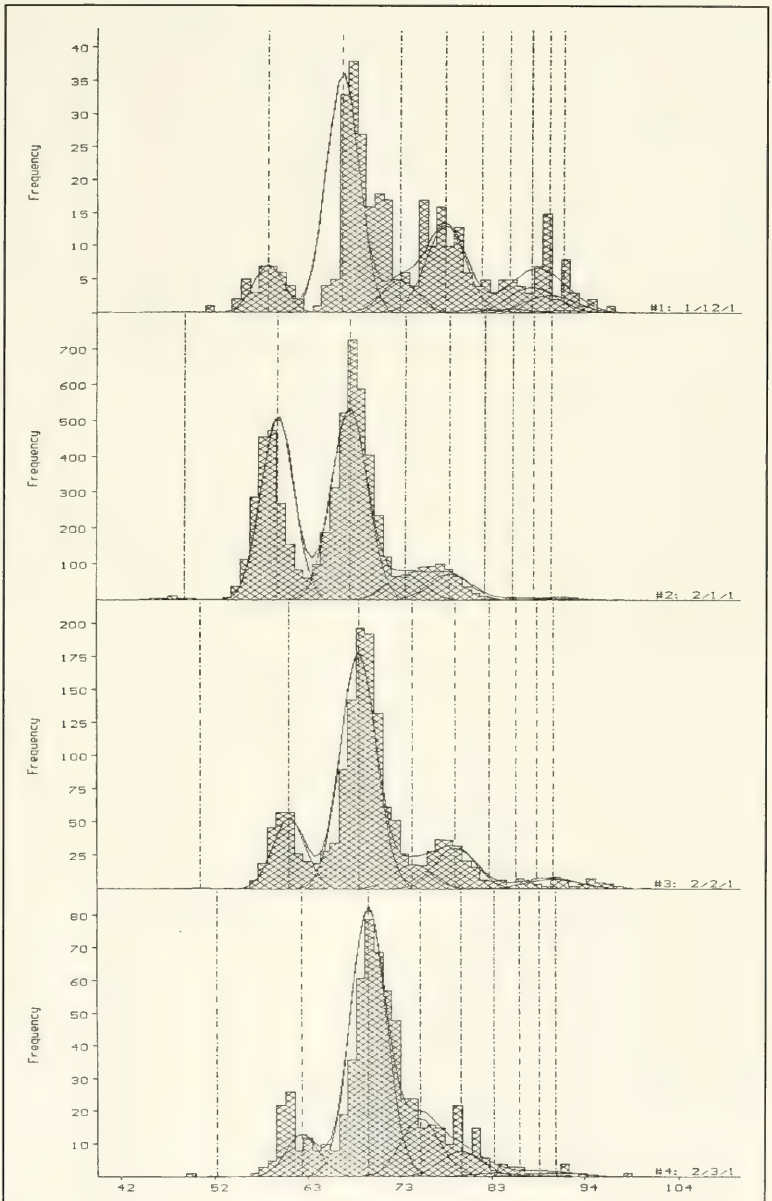
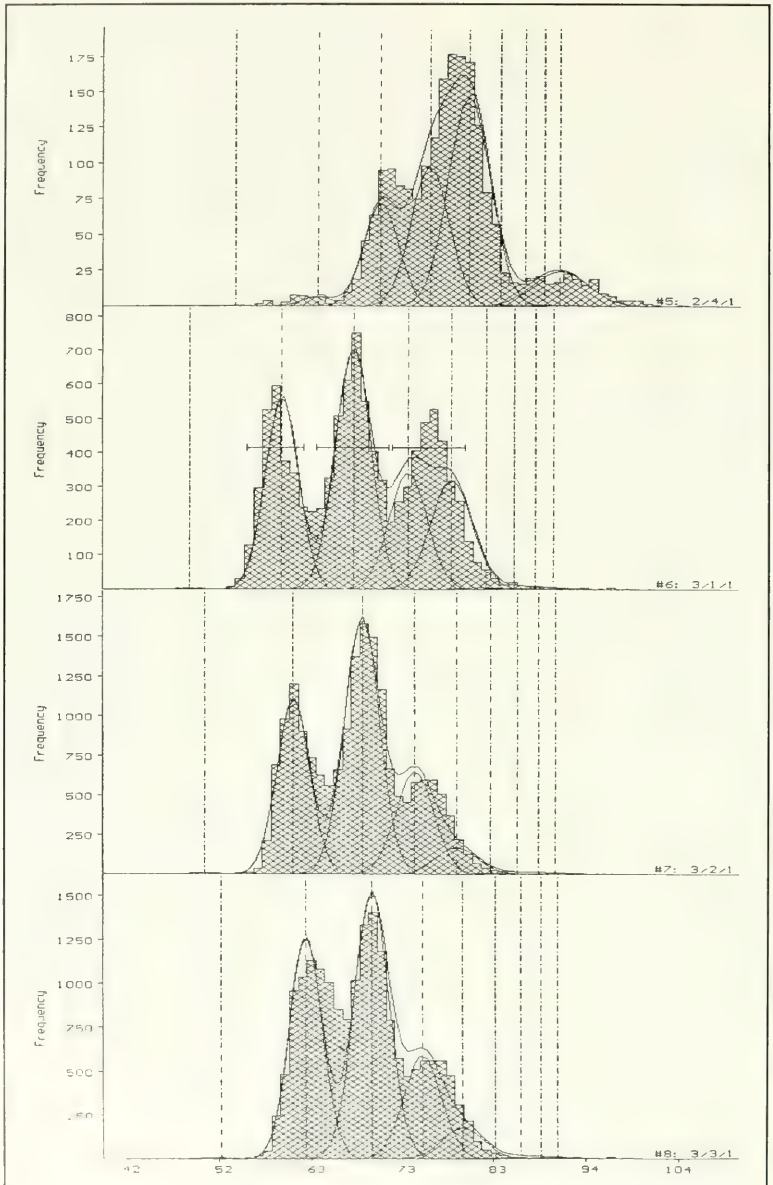


Figure 2

The south Pacific albacore length-frequency data set. The corresponding sampling period are given in the lower right of each histogram. The sampling data format is year/month/week; year 1 was 1988. No sampling was conducted during December 1989. The horizontal bars over the first three modes of sample no. 6 correspond to the user supplied bounds on the mean length of these age classes. The dashed vertical lines represent the estimated mean lengths-at-age in each sample. The inner smooth curves are the estimated numbers at age and the outer smooth curve is the estimated frequency distribution.



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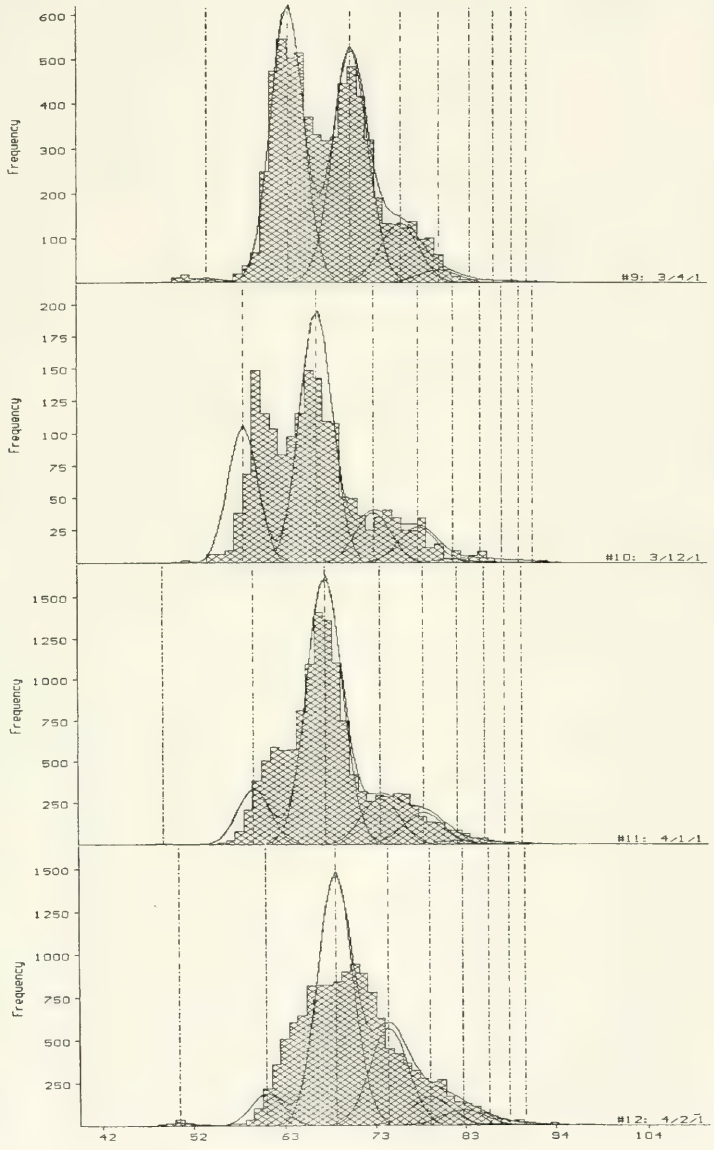

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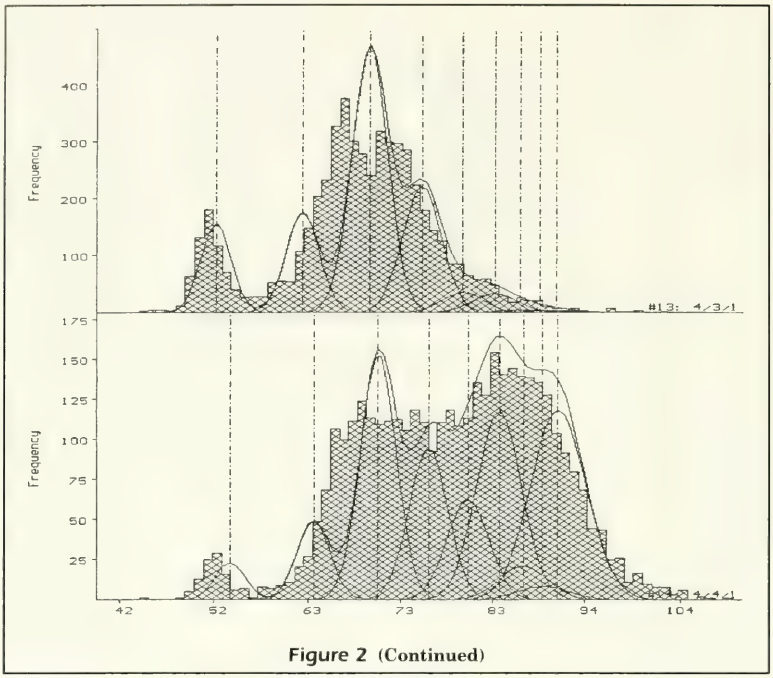

Figure 2 (Continued)

(Fig. 1). Altogether, 494 vertebrae were collected, of which 66% were from troll-caught albacore. All albacore sampled were first measured according to the procedure described previously. Vertebrae were removed by severing the caudal peduncle immediately anterior to the large bony keels. Vertebrae in the caudal peduncle were selected because they were easy to collect and their removal did not affect the market value of the fish. The caudal fins were trimmed, and the entire peduncle was placed in a plastic bag and frozen. Sex was recorded as often as possible (128 cases), but logistic difficulties prevented internal examination of the majority of the albacore sampled.

All vertebrae were processed in the laboratory according to the methods described by Berry et al. (1977), Berry (1978), and Lee et al. (1983). Caudal peduncles were thawed and the flesh trimmed from around the vertebrae. The 35th and 36th vertebrae were separated from the others with a knife and a fine-toothed hand saw. Each vertebra was then clamped in a vise by the keel, and sawed in half along the sagittal (dorsoventral) plane. Remnants of the cone jelly were removed and the anterior portion of the cone was lightly scrubbed.

The left lateral section was normally used for staining unless it had been damaged by cutting. Sections were soaked for 5–20 minutes in Alizarin red-S stain with Berry's (1978) "school tuna" solution, and then rinsed in fresh water. Sections stained too darkly were soaked in a 5% hydrogen peroxide solution until the stain faded sufficiently. Stained vertebrae examined under high intensity visible light displayed distinct band couplets on the anterior cone (see Johnson, 1983). Within each couplet, the bands are uniformly spaced around the cone and separated by a thin translucent zone. Each couplet is separated from adjacent ones by a wide opaque zone that becomes somewhat depressed towards the outside edge of the cone. Each couplet of twin bands was considered to be a distinct growth ring. The vertebral-ring-count was given by the number of complete couplet bands observed.

The investigators examined 20 stained vertebrae to derive criteria to be used in interpreting the ring structures. Vertebrae were then processed by the team: one biologist read 20 vertebrae while the other recorded data, and vice versa. At least 25% of the samples processed each day were examined by both persons to check consistency. Identical counts were obtained in

>95% of the cross-checks; samples were rejected if the discrepancies in counts could not be resolved. A linear relationship (r^2=0.94) was detected between ring counts for the 35th and 36th vertebrae of the first 200 albacore processed, and no significant difference in age composition was found between counts from the two sets of vertebrae (χ^2 test, P=0.9). Even though the 35th and 36th vertebrae were both suitable for study, we chose the 35th vertebrae because it was larger and easier to read in most cases.

Tagging operations

For tagging, albacore were caught mainly with commercial troll gear (Dotson, 1980). The tagging procedure was similar to that described by Laurs et al. (1976). Immediately after a strike, the fishing line was retrieved manually. Once the specimen was on board, the hook was removed and the albacore was quickly inspected for injuries to the gills, eyes, mouth, and palate. Albacore that were vigorous and not visibly injured were placed on a measuring board or tagging cradle (Kearney and Gillett, 1982) and were tagged as rapidly as possible with a stainless steel tube applicator that contained a 13-cm-long serially numbered spaghetti-type plastic tag with a single barbed nylon head. The tag was inserted at an oblique angle so that the barb was anchored among the pterygiophores of the second dorsal fin. Fork length was measured and recorded on audio tape, along with the date, time, albacore condition, and tag number. Albacore were returned to the water head first immediately after tagging.

Labelle (1993b) described the albacore tagging operations conducted in the south Pacific, and summarized the corresponding release-recapture statistics. Approximately 17,000 albacore were tagged and released from troll fishing vessels during 1986–92; the season totals ranged from 815 to 6,524. As of November 1992, recaptures of 42 tagged albacore had been reported; we obtained complete information on sizes and dates of release and recapture for 27 of 42 albacore. Most of these 27 tags were returned by fishermen, although some were detected during catch sampling at canneries and landing sites. Recreational fishermen also tagged and released an additional 3,646 albacore along the south east coast of Australia during 1973–92 (Matthews and Deguara, 1992). As of November 1992, 14 of these had been recovered but only one tag recovery record was sufficiently complete to allow inclusion of the data.

Data analysis

Length-frequency analysis The MULTIFAN computer program was used to estimate VB growth parameters from the length-frequency data under the assumption that the modes in the data represent year classes. A detailed description of the model is given by Fournier et al. (1990) and the program is described in the MULTIFAN 3 *User's Guide and Reference Manual* (Otter Research, 1991). MULTIFAN can incorporate specific structural hypotheses into models being fitted to the length-frequency data. The simplest structural hypothesis assumes that the mean lengths-at-age lie on a VB growth curve and that the standard deviations of length-at-age are identical for all cohorts. More complex structural hypotheses can be tested to determine if they provide a statistically significant improvement in fit to the data. The more complex hypotheses tested assume that the following processes can occur in the population sampled:

1 Sampling bias for the first cohort. This could result from selectivity during the sampling process induced by the fishing gear or the sampling method. Size selectivity was assumed to apply only to the first cohort and to decrease linearly with age until fish reach the second cohort.
2 Age-dependent standard deviation in length-at-age. For some fish populations, variation in length-at-age is not constant across cohorts. This hypothesis allows the standard deviation of length-at-age to increase or decrease linearly with age.
3 Seasonally oscillating growth. Seasonal growth patterns are known to occur in some fish populations (Pauly and Gaschütz, 1979). This process was incorporated into the growth model by adding two parameters, one representing the magnitude of the seasonal effect and the other determining the time of the year at which growth is slowest because of the seasonal effect.

We systematically fitted models incorporating all possible combinations of the above structural hypotheses and used likelihood ratio tests to identify the most parsimonious model structure. Fitting and testing procedures were done automatically by MULTIFAN, although some user-specified input was needed to ensure that the model exhibited stable behavior (see Fournier et al., 1990, for explanations).

Estimates of the VB growth parameters K and L_∞ were obtained along with parameters for sampling bias, age-specific standard deviations, and seasonal growth. In the absence of information on the age of the first age-class, MULTIFAN assumes that the VB curve passes through the origin (i.e., t_0=0). Estimates of age-at-length are based on this assumption.

Analysis of vertebrae data The VB growth parameters were estimated from vertebral-ring-count data and length data, under the assumption that ring counts indicate total age (in years). We did not attempt to

estimate fractional age based on an assumed birth date; therefore, all ages are integers. Maximum-likelihood estimates (MLE) were obtained according to the procedure described by Kimura (1980). The objective function (Φ) minimized to obtain the parameter estimates was the negative log-likelihood of the VB model:

$$\Phi = \frac{N \log_e (2\pi\sigma^2)}{2} + \frac{\sum_{i=1}^{N} \{l_i - [L_\infty (1 - e^{K(t_i - t_0)})]\}^2}{2\sigma^2} \quad (1)$$

where: l_i = fork length of individual i,
t_i = presumed age of individual i,
N = number of individual measurements,
L_∞ = estimated asymptotic fork length,
K = estimated growth coefficient,
t_0 = estimated hypothetical age at zero length,
σ^2 = estimated variance associated with the length-at-age.

The objective function was minimized by using the Quasi-Newton algorithm in the NONLIN statistical module of the SYSTAT microcomputer program (Wilkinson, 1989). Asymptotic standard errors and parameter correlations were obtained from the Hessian matrix once the iteration process was complete (see Wilkinson, 1989). As suggested by Kimura (1980), the initial values supplied for the parameters were obtained from the Walford plot (Ricker, 1975).

Comparison of growth curves with tag-return data

We used the growth curves fitted to the two data sets and the observed length increments from the available tag-return data to test our assumption that the length-frequency modes represent year classes and vertebral-rings represent annual features. It must be acknowledged that there is no statistically correct means of comparing the models and the length increment data, because the growth curves derived from length frequencies and vertebral-ring-counts are based on age-length data. The only statistically correct predictions possible from these growth models are predictions of length (the dependent variable) from age (the independent variable). However, the length increment data can be related to the growth curves by first generating predictions from the fitted growth models which are then compared to the length increment data. This was accomplished by predicting lengths-at-recapture by using the standard Fabens (1965) length increment model:

$$l_{r_i} = l_i + (L_\infty - l_i)(1 - e^{-K\Delta_t}) \quad (2)$$

where: l_i = length at release of individual i,
Δ_{t_i} = time at liberty of individual i,
l_{r_i} = estimated length-at-recapture of individual i,

and L_∞ and K are the VB parameters estimated from the length-frequency or vertebral-ring-count data. As noted above, this procedure is not correct in the strict statistical sense because the growth models are not used to predict length from age (see Francis, 1988). However, for comparative purposes, the second method should reveal any gross departures from the "annual features" assumption applied in fitting the growth models. Some justification for this is presented later.

Results

Growth analysis based on length-frequencies

The most parsimonious model structure for the albacore length-frequency data set included seasonal growth and age-dependent standard deviation in length-at-age. The incorporation of first length bias did not significantly improve the fit. Parameter estimates and estimates of the means and standard deviations of length-at-age are given in Table 1. Note that we use the term "relative age class" to denote that estimates of absolute age are based on the assumptions that the length modes represent annual cohorts and t_0=0.

The seasonal growth phase estimate of 0.216 indicates that fastest growth occurs in February, and slowest growth occurs six months later in August at the end of the austral winter. The seasonal growth amplitude estimate (0.949) is near the upper limit of 1.0, indicating that growth is almost non-existent at that time of the year. Standard deviation in length-at-age increased progressively with age for the nine significant age classes detected.

The predicted aggregate length-frequency distributions fitted the observed distributions very well over the entire range of sizes (Fig. 2), and the predicted modes closely matched the actual modes in most months. The predicted modal distribution pattern indicates that there were usually four prominent age classes in troll catch samples.

Growth analysis based on vertebral-ring counts

The fork lengths of the albacore sampled ranged from 44 to 110 cm (Table 2), which corresponds to the size range of albacore caught in the surface and longline

Table 1
Estimated parameters from the MULTIFAN analysis, with predicted fork lengths (FL) and standard deviations (SD) of lengths-at-age.

Parameter	Estimated value	Relative age class	Predicted FL ($\hat{x}$, cm)	Length-at-age SD
von Bertalanffy K (cm·yr^{-1})	0.239	3.04	48.86	1.74
von Bertalanffy L_∞	97.100	4.04	59.12	2.03
Brody's rho (ρ)	0.788	5.04	67.19	2.29
Age of first age class (yr)	3.040	6.04	73.55	2.53
Mean length sampling bias	0.000	7.04	78.56	2.72
Seasonal growth phase	0.216	8.04	82.50	2.89
Seasonal growth amplitude	0.949	9.04	85.60	3.03
Mean SD	2.373	10.04	88.05	3.14
Ratio of first to last SD	1.861	11.04	89.98	3.24

Table 2
Summary statistics on sizes of albacore aged from vertebral-ring-counts.

Ring count	Sample size	Range (FL, cm)	Mean FL	Length-at-age SD	Coefficient of variation	Mean size increment
1	7	45–51	47.2	2.21	4.68	—
2	79	44–65	50.1	4.23	8.38	2.9
3	71	46–72	57.1	6.86	12.03	7.0
4	68	48–78	65.9	6.63	10.01	8.8
5	61	57–95	73.6	8.01	10.88	7.7
6	53	58–99	79.6	8.74	10.98	6.0
7	54	70–105	85.1	8.42	9.89	5.5
8	26	73–102	88.9	7.34	8.25	3.8
9	20	80–101	95.0	4.58	4.81	6.1
10	32	88–110	96.6	4.61	4.77	1.6
11	20	92–107	97.6	3.69	3.78	1.0
12	2	103–108	105.5	3.53	3.35	7.9
13	1	107–107	107.0	—	—	1.5

fisheries (Labelle, 1993a). Up to 13 rings, assumed to be annuli, were visible in the vertebrae sampled. Sample sizes for all relative age classes were greater than 20, except for classes 1, 12, and 13. Significant differences in the standard deviation of length-at-age were detected among the age classes (Bartlett's test, χ^2=64.683, P<0.001), and the standard deviation was greatest for relative age classes 5–7. This trend differs from the results obtained in the length-frequency analysis, which indicated increasing standard deviation with age (although only linear trends were possible in this analysis).

Differences in mean size between the successive age classes were calculated to reveal other anomalies in growth patterns. In theory, absolute growth should be rapid at first and decrease progressively in later life (see Ricker, 1975). The pattern observed for albacore agrees with these theoretical expectations, except for the high growth rates observed between relative ages 8→9 and 11→12 (Table 2). No statistical or biological criteria justified the omission of the data associated with ages 8→9 from the analysis. However, the large growth increment obtained for age 11→12 could simply be biased because of the small sample size (2) for relative age class 12.

The VB model was fitted to the aggregate vertebral-ring-count data for relative age classes 2–11. The data for relative age classes 1, 12, and 13 were excluded because of their small sample sizes. The VB model provided a good fit to the remaining data (Fig. 3). The residuals were generally well centered around zero and the slope of a linear regression of residuals against relative age was not significantly different from zero (F-test=0.001; P=0.973).

Of the albacore sexed, 59 were females and 70 were males. As these were distributed in a similar fashion with respect to relative age class as the pooled data set (females, males, and unsexed), the VB parameters were estimated for each sex (Table 3). Likelihood ratio tests (Kimura, 1980) were used to test for differences in growth parameters between sexes. No significant differences were detected for any of the tests carried out (Table 4). Therefore, the growth parameters estimated from the pooled data set were considered to be representative of growth patterns of male and female albacore within the size range sampled.

Comparison of growth curves

A direct comparison of the VB growth curves estimated from length-frequencies and vertebral-ring-counts is slightly complicated by the assumption of t_0 = 0 for the length-frequency analysis and the estimation of t_0 = −1.922 year for the vertebral-ring model. This inconsistency would result in the growth curves being out of phase by almost two years, apart from any other differences that might be present. One way of comparing the two curves is to compare the expected growth of

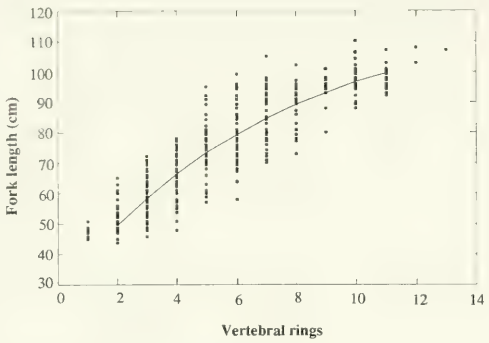

Figure 3

Observed albacore fork lengths (cm) for each ring-count category (relative age class). The von Bertalanffy curve fitted to data for relative age classes 2–11 is represented by the solid line.

an albacore of a specific initial size over time. This is equivalent to using the L_∞ and K estimates in a Fabens-type length increment model to make an approximate comparison of predicted growth trends independent of assumed or estimated t_0. Despite substantial differences in the L_∞ and K estimates from the two analyses, there was little difference in the predicted growth of a 40-cm albacore over time within the range of the data (Fig. 4).

Growth rates of tagged albacore

The 28 tag release-recapture records with complete growth data included a wide variety of sizes (61.0–96.5 cm), times-at-large (54–1,790 days) and release-recapture locations well distributed throughout the principle fishing areas. Estimated average growth rates during the periods at large were 0.17–1.13 cm·month^{-1}. For albacore at liberty <500 days, growth rate showed the expected decline with increasing mid-size (half way between release and recapture sizes); but this decline was negligible for albacore at liberty >500 days (Fig. 5). Given the relatively small number of records available, no attempt was made to estimate the VB growth parameters based on tag release-recapture data.

Comparison of tag return growth increments with the fitted models

To compare the consistency of the VB models derived earlier with the tag-return data, we first calculated sets of predicted recapture lengths for the 28 tag return records by using the two sets of L_∞ and K estimates, derived from length-frequency and vertebral-ring-count data, in Equation 2. We also made a third set of predictions using the L_∞ estimate and twice the K estimate obtained from the length-frequency analysis (L_∞=97.1 cm, K=0.478 yr^{-1}). These parameters are consistent with an assumption that the observed

Table 3

MULTIFAN parameter estimates of the VB growth model based on the vertebral-ring-counts. Parameter estimates are based on all albacore of relative ages 2–11 (top); females only of ages 2–9 (middle); and males only of ages 2–10 (bottom). Lower and upper bounds are the upper and lower limits of the 95% confidence intervals. MLE=maximum-likelihood estimates.

Sample content	Parameters	MLE	SD	Lower bound	Upper bound	Correlation matrix		
						L_∞	K	t_0
All albacore	L_∞	121.024	5.193	110.846	131.202			
ages 2–11	K	0.134	0.016	0.104	0.165	–0.981		
n = 484	t_0	–1.922	0.291	–2.492	–1.350	–0.880	0.951	
	σ^2	46.102	2.964	40.293	51.910	0.004	–0.004	–0.004
Females	L_∞	169.320	54.532	62.440	276.200			
ages 2–9	K	0.077	0.045	–0.011	0.166	–0.994		
n = 58	t_0	–2.573	1.109	–4.745	–0.400	–0.900	0.940	
	σ^2	40.775	7.574	25.930	55.621	0.026	–0.026	–0.024
Males	L_∞	122.037	14.332	93.947	150.127			
ages 2–10	K	0.168	0.054	0.063	0.274	–0.980		
n = 70	t_0	–0.907	0.649	–2.179	0.365	–0.847	0.929	
	σ^2	64.262	10.862	42.972	85.551	0.002	–0.002	–0.002

Table 4

Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) albacore, based on the procedure described by Kimura (1980).

Hypothesis	Linear constraints	Parameter estimates $L_{\infty 1}$	$L_{\infty 2}$	K_1	K_2	$t_{0,1}$	$t_{0,2}$	Residual SS	χ^2	df	P
1	none	122.037	169.320	0.168	0.077	−0.907	−2.573	6863.3			
2	$L_{\infty 1}=L_{\infty 2}$	129.504	129.504	0.145	0.134	−1.180	−1.561	6911.0	0.104	1	>0.70
3	$K_1=K_2$	131.088	127.932	0.140	0.140	−1.265	−1.455	6922.4	0.129	1	>0.60
4	$t_{0,1}=t_{0,2}$	131.197	128.411	0.138	0.141	−1.350	−1.350	6933.6	0.153	1	>0.50
5	Same L_∞, K, t_0	131.157	131.157	0.136	0.136	−1.385	−1.385	6948.1	0.184	3	>0.50

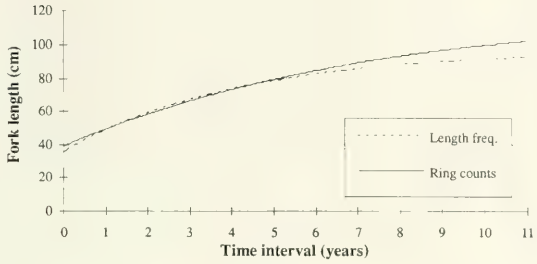

Figure 4

Growth of south Pacific albacore from an initial length of 40 cm as predicted by models fitted to length-frequency and vertebral-ring-count data.

Discussion

Estimates of the VB growth parameters for south Pacific albacore based on the analysis of length-frequencies and vertebral-ring-counts were generally within the ranges of values reported for albacore from other regions (Table 5). The only exception was the L_∞ estimate obtained with MULTIFAN, which was lower than all other estimates reported. This could be partly due to the fact that the data set used for the MULTIFAN analysis did not include length-frequency samples from longline catches, so the largest size classes were not well represented. Nevertheless, we do not attach any biological significance to this or to the differences in VB parameters estimated from the two data sets in this study. Despite differences in the parameters, the predicted growth patterns based on the two analyses are remarkably similar. This often noted feature of the VB growth model (e.g., Knight, 1968; Francis, 1988) highlights the potential pitfalls of comparing growth only on the basis of VB growth param-

length-frequency modes are semestral, rather than annual features. We then compared each set of predictions to the observed recapture lengths.

The growth models derived from length-frequency and vertebral-ring-count data, assuming that the modes and rings are annual features, appear to be consistent with the tag return length increment data (Fig. 6). Deviations of observed from predicted recapture lengths are both positive and negative and are generally within the range of expected individual variation. In contrast, the growth model based on the assumption of semestral length-frequency modes overestimates the recapture lengths. On this basis, the tag return length increment data lend support to our initial assumptions concerning the length-frequency modes and vertebral-rings.

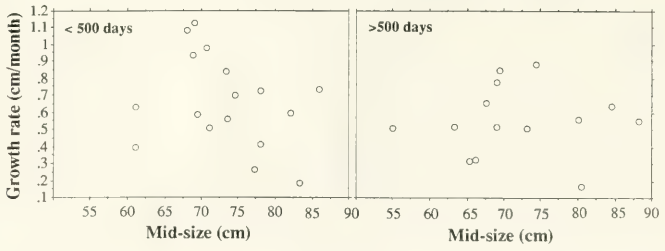

Figure 5

Individual growth rates of tagged south Pacific albacore for two time-at-liberty categories. Mid-size is the fork length half way between the release and recapture lengths.

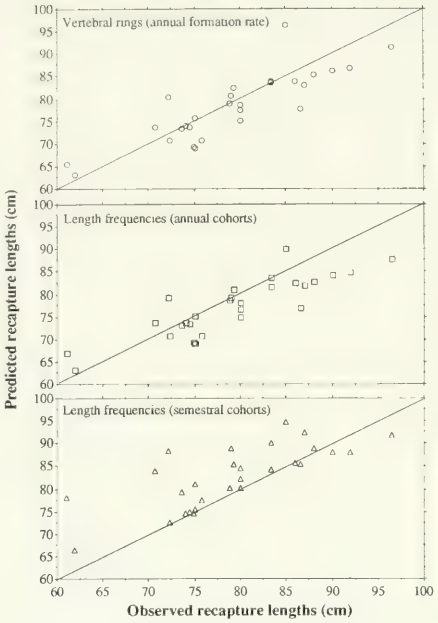

Figure 6

Predicted versus observed recapture lengths of tagged south Pacific albacore. The three panels depict recapture lengths predicted on the basis of models fitted to length-frequency data assuming annual cohorts, vertebral-ring-count data assuming an annual formation rate, and length-frequency data assuming semestral cohorts. The lines cover the points corresponding to a perfect match between predicted and observed lengths.

eters. In this study, the VB model was preferred to alternatives because it was used in available software such as MULTIFAN. There were no indications from the data that the VB model was not appropriate for modelling albacore growth, although a Gompertz model (Ricker, 1979) appeared to provide an equally good fit to the vertebral-ring-count data.

In fishes, rings are thought to form in bony tissues as a series of growth checks separated by zones, usually more opaque, that are associated with growth (Casselman, 1983). The usual inference that rings are formed yearly is based on the observation that growth rate, particularly for temperate species, is frequently seasonal as a result of its dependence on temperature. Growth checks are thought to occur during the period of the year when the water is coldest; high growth rates occur during periods of warmer water temperatures. Length-frequency analysis provided evidence that juvenile albacore growth is strongly seasonal; therefore this seasonality could be the basis of ring formation in vertebrae. However, the relationship of water temperature with this seasonality is unknown. Albacore, while being predominantly a temperate species, are also found in tropical waters, particularly as adults. In common with other *Thunnus* species, they occupy a three-dimensional habitat within wide temperature limits (14–20°C) and are capable of physiological thermoregulation, maintaining body temperatures of up to 15°C warmer than that of the surrounding waters (Morrison et al., 1978). It is possible that ring formation in the bony tissues of albacore is influenced by these biological characteristics and by more complex biological cycles, such as feeding and reproduction, as well as the temperature of the water that they occupy.

As a working hypothesis, the length-frequency modes and vertebral-rings were assumed to be formed each

Table 5

Reported estimates of the von Bertalanffy growth parameter albacore from various regions around the world.

Data source	Sampling region	Aging method	L_∞	K	t_0	Size range (FL, cm)
Clemens (1961)	N. Pacific	Tagging	135.6	0.170	−1.870	54–77
Shomura (1966)	N. Pacific	Tagging	118.8	0.250	1.999	60–91
Shomura (1966)	N. Pacific	Scales	114.4	0.308	0.818	65–120
Shomura (1966)	N. Pacific	Scales	145.3	0.159	−0.056	50–120
Laurs and Wetherall (1981)	N. Pacific	Tagging	125.0	0.199	—	47–92
Shomura (1966)	N. Pacific	Vertebrae	104.8	0.431	1.504	69–90
Shomura (1966)	N. Pacific	Scales	145.3	0.150	−0.396	40–95
Bell (1962)	N. Pacific	Scales	108.8	0.225	−2.273	51–94
Huang et al. (1991)	Indian	Scales	128.1	0.162	−0.897	64–106
Beardsley (1971)	Atlantic	Length data	140.0	0.141	−1.830	68–114
González-Garcés and Farina-Perez (1983)	N. Atlantic	Dorsal spine	140.1	0.129	−1.570	38–110
Santiago (1992)	N. Atlantic	Length-freq.	117.9	0.200	—	48–106

year in the growth models presented in this paper. Laurs et al. (1985) validated the daily increment formation rates in sagittae of tagged north Pacific albacore that had been injected with oxytetracycline (OTC) prior to release and concluded that the increment counts, adjusted upwards by 5%, provided an accurate estimate of absolute age. Preliminary estimates of absolute age of south Pacific albacore were obtained from counts of otolith increments, assuming similar increment deposition rates as for the north Pacific population (Wetherall et al., 1989). These results indicated that south Pacific albacore grew about twice as fast as our estimates suggest. This would suggest that the length-frequency modes and vertebral-rings analysed here are more likely to be semestral than annual features.

The length increment data from 28 tag returns presented in this study clearly favor the hypothesis of annual length-frequency modes and vertebral-rings over a semestral formation rate. Given the assumption that length-frequency modes represent cohorts of albacore spawned during the same season, we would expect the temporal spacing of length-frequency modes to correspond to the frequency of spawning seasons. Both gonadosomatic indices and microscopic examination of gonad tissue of south Pacific albacore clearly indicate a single annual peak in spawning activity during the austral summer (Ramon and Bailey, 1993).

Most of the evidence therefore points towards annual length-frequency modes and vertebral-rings, although the conflicting results obtained from "daily" growth increment counts on otoliths are deserving of further study. It would be particularly useful to estimate increment formation rates in vertebrae and otoliths of tagged south Pacific albacore injected with OTC before release, as was done for the north Pacific population. During 1986–1989, 3,341 tagged south Pacific albacore were injected with OTC, and to date, three have been recaptured and the relevant hard parts obtained. It is hoped that examination of this material will, in due course, clarify increment deposition rates in south Pacific albacore.

A previous review of the available information on stock structure lead Lewis (1990) to conclude that the south Pacific population probably had very limited exchange with those of the North Pacific and the Indian Ocean. Parasite studies (Jones, 1991), tagging programs, and ongoing electrophoretic surveys have not yet revealed the existence of separate sub-stocks within the south Pacific population. Thus, the growth rates reported here could be considered as representative of the growth patterns in the entire south Pacific albacore population. However, we cannot reject the hypothesis that populations from other oceans have significantly different growth patterns. It is also plausible that local phenomena, such as land mass effects and upwelling zones that can affect the growth rates of albacore within certain regions of the south Pacific.

Acknowledgments

Several persons and agencies have contributed significantly to this research. Staff of the South Pacific Commission (SPC), New Zealand Ministry of Agriculture and Fisheries (MAF), and the United States National Marine Fisheries Service have contributed to the tagging, observer, and port sampling programs. Special thanks go to Patrick Swanson of MAF for his assistance in aging the vertebrae. We also thank all troll fishermen who assisted with the observer program and the release and recovery of tags. Financial assistance for the observer and tagging programs and for the data processing and analysis was provided by the European Community Fifth European Development Fund and the Canadian International Center for Ocean Development.

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Reproductive biology of the false southern king crab (*Paralomis granulosa*, Lithodidae) in the Beagle Channel, Argentina

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Abstract.—Reproduction of the false southern king crab (*Paralomis granulosa*) in two localities of the Beagle Channel, Argentina, was studied by monthly trap sampling during 1989 and 1990. Size at gonadal maturity in males (50.2-mm cephalothoracic length, CL) and females (60.6-mm CL) was significantly less than size at morphometric maturity (57.0-mm CL in males; 66.5-mm CL in females). Embryonic development lasted 18–22 months. During this period, there was apparently a 10–12 month diapause. In one of the two localities, development of eggs in a given clutch was very heterogeneous, suggesting simultaneous occurrence of eggs with 12- and 22-month development periods. Larval hatching took place mainly during winter. Female *P. granulosa* molted during November and mated immediately after. Biennial reproduction was detected on the basis of ovarian and embryonic development, and on the basis of shell condition. Thus, two different female groups occur in the population of the Beagle Channel. Fecundity increases with size (1,441 to 8,110 eggs per female) and is significantly less at the end than at the start of embryogenesis. Ovaries and brood each represented at most 6–7% of body weight. *Paralomis granulosa* is the only representative of its genus that inhabits shallow water and apparently retains some reproductive features of its deep-water relatives.

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Crabs of the genus *Paralomis* are lithodids that inhabit the Atlantic, Indian, and Pacific Oceans, ranging in depth from 5 to 4152 m. The false southern king crab, or centollón in Spanish, *Paralomis granulosa* (Jacquinot, 1847), inhabits the Pacific Ocean from Paso Tenaún (Chile; 40°S) to Cape Horn, and the Atlantic Ocean from 56°S to the Golfo San Jorge (Argentina; 47°S) including the Islas Malvinas (Falkland Islands) at depths of up to 50 m (Macpherson, 1988).

Paralomis granulosa and the southern king crab (*Lithodes santolla*) constitute the main crustacean fisheries off the southern tip of South America. Commercial exploitation of *P. granulosa* started in the early 1970's. The largest catches were recorded in 1986 and amounted to 1,300 metric tons for Argentina and Chile. In Argentina, during the last three years, the yield of *P. granulosa* was at least twice as great as that of *L. santolla*. Although commercial fishing for *P. granulosa* began more than 15 years ago, studies on the life history of this species are few. Management studies were conducted in Chile which resulted in fishing regulations, such as a minimum legal size and gear restrictions (Campodónico et al., 1983). There is virtually no information on the life cycle of *P. granulosa* in South America, except for reports on larval development (Campodónico and Guzmán, 1981), larval ecophysiology (Vinuesa et al., 1989), and diets of juveniles and adults (Comoglio et al., 1990).

In this study we document aspects of the reproductive biology of *P. granulosa*, from data collected during monthly sampling in the Beagle Channel during 1989 and 1990. Data on the reproductive cycle, fecundity, embryogenesis, and other life history traits were examined to acquire basic information on the biology of this commercially valuable species.

Materials and methods

The fishing area was located along the Beagle Channel between Lapataia Bay (west) and the Moat Channel (east) (Fig. 1): fishing depths ranged from 10 to 60 m. The Beagle

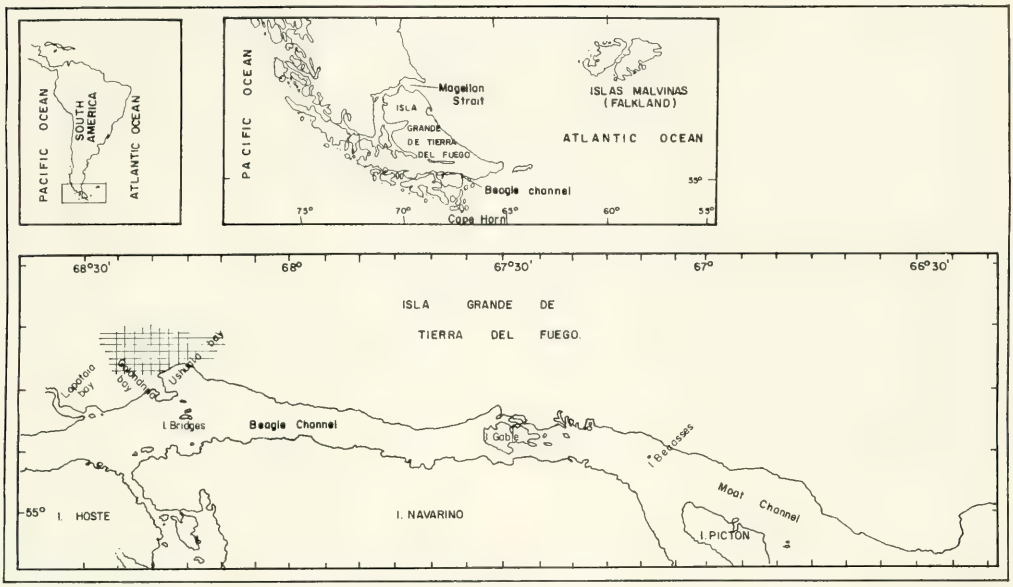

Figure 1
Location of sampling area.

Channel is an elongate glacial valley which stretches east-west, extending between the Isla Grande de Tierra del Fuego, and Navarino and Hoste Islands (Rabassa et al., 1986). It is 210 km long and on average 4 km wide and has a maximum depth of 160 m. Surface seawater temperatures range from 4.2 to 4.3°C in August and from 8.9 to 9.8°C in January; the annual mean temperature varies from 6.5 to 6.8°C. Salinity ranges from 26.7‰ in November–December to 31.3‰ during July and is highly variable during October and November because of ice melt.

Monthly samples were obtained from commercial catches from January 1989 to December 1990. Crabs were captured in traps deployed on bottom lines with 10 traps each. Traps were fished for 48 hours and usually baited with chicken, fish, horse, pig, cow, or lamb meat and bones. Each month 30–40 females and 10 males were randomly selected from the catch of a single line, placed in tanks with circulating seawater and transported alive to the laboratory. Carapace length (CL, midline distance between posterior orbital margin, excluding the rostral spine, and the posterior median margin) and right chela height (CH, measured at the anterior dorsal margin of the propodus, between the two anterior spines) of each crab were measured to the nearest 0.1 mm with a vernier caliper. Live body weight was measured to the nearest 0.01 g. The carapace of each crab was aged according to the following subjective scale:

1 Postmolt (POM): Shell soft, bright red, membranous and non-calcified, without epibiota.

2 Early Intermolt (EIM): Shell hard but brittle, bright red, without epibiota.

3 Median Intermolt (MIM): Shell hard, red to brown, variably covered with epibiota such as serpulids.

4 Advanced Intermolt (AIM): Shell hard, dark red, with numerous epibionts including balanids (6–8 mm maximum basal diameter), bivalves (*Mytilus edulis, Aulacomya ater*, 4–6 mm length), serpulids, and other calcareous polychaetes, bryozoans, and brown algae.

5 Premolt (PRM): Similar to AIM but the old shell is partially raised, revealing the new shell.

For both sexes, we used two methods to determine the size at which 50% of individuals were mature:

- Analysis of reproductive features. Females were considered to be mature if they had eggs or empty egg cases attached to the pleopods; males were considered to be mature if spermatophores were found in their vas deferens. The proportion of mature individuals was calculated for each 5-mm-CL interval and a logistic function was adjusted to provide 50% maturity.
- Allometric growth of the right chela. This method is based on the relative change in chela height at sexual

maturity (Hartnoll, 1978). We used MATURE1, the computer method described by Somerton (1980) to fit a pair of intersecting straight lines to plots of chela height on carapace length. The method determines the regression lines for crabs that are assumed to be immature and mature, based on minimum observed size at gonadal maturity and maximum size at gonadal immaturity, respectively. Then it extends the lines to the central area of the plot, where immature and mature crab are mixed, by iteratively assigning each point to either line, then recalculating lines, until no points switch lines on two successive iterations. On the basis of this classification, the proportion of mature individuals was calculated for CL-size intervals of 5 mm in males and of 4 mm in females and a logistic function was adjusted to provide 50% maturity (Wenner et al., 1974). Measurements of partially regenerated chelae were excluded from this analysis. Data for crabs <50 mm CL were obtained from a study of juvenile growth (Lovrich, 1991).

Fecundity was defined as the number of eggs per clutch. In the laboratory, pleopods with attached eggs were removed from each female and preserved in buffered 10% formalin in seawater. Later the eggs were detached from the pleopods and the clutch was blotted and weighed to the nearest 0.01 g (*WC*). Three subsamples were then weighed to the nearest 0.01 g (*ws*) and eggs in each subsample were counted (*ns*). Fecundity (*F*) was calculated as:

$$F = \sum_{i=1}^{3} [(WC * ns)/ws] / 3 .$$

Estimates of fecundity based on counts of three subsamples did not vary by more than 5%.

Egg characteristics, color, developmental stage, presence of chromatophores and appendage development were determined monthly with the aid of a stereoscopic microscope. Fifteen *P. granulosa* females were kept in a 600-L and 250-L tank in a controlled-environment room with photoperiod, temperature, and salinity adjusted to natural environmental variations from April 1990 to May 1991. Crabs were fed *ad libitum* with limpets, mussels, and fish 2–3 times a week. A subsample of 15–20 eggs was taken from each egg mass at weekly intervals at the beginning of the study and at monthly intervals thereafter. Eggs from females kept in the laboratory and eggs preserved in formalin were separated, and the maximum diameter of each egg was measured to the nearest 0.01 mm with an ocular micrometer.

Ovaries were removed and weighed to the nearest 0.01 g. Two portions of the ovary were sampled: one was stored in buffered 10% formalin in seawater and the other was fixed in Bouin's solution and later transferred to 70% ethanol. The latter portion was then embedded in paraffin, sectioned at 8–10 μm and stained with "one time" trichrome (Gabe, 1958). Ovarian development was described in two ways: 1) the gonadosomatic index was the ratio weight of ovaries : total body weight, multiplied by 100; 2) mean diameter of oocytes was determined from measurements of 30 to 40 of the roundest oocytes from the periphery of the formalin-preserved ovary by using an eyepiece micrometer on a compound microscope.

Ten to 12 males were dissected bimonthly to check for the presence of spermatophores in the vas deferens. The right vas deferens was stored in 10% formalin and later pressed between a slide and coverslip to detect spermatophores under a microscope.

Data were $\log_{10}$-transformed to obtain normality and to reduce heteroscedasticity. Simple correlations and predictive regressions were then calculated for selected life history traits. Outliers were detected by comparing the values of the standardized residuals from the regression line to Student-*t* tabulated values. Slopes and elevations of regressions were compared by analyses of variance (ANOVA) and of covariance (ANCOVA), respectively (Sokal and Rohlf, 1981).

Discriminant analysis was used to determine the existence of two groups in ovarian development data. We then classified each crab into either group on the basis of an objective decision rule (Morrison, 1976). Variation in oocyte diameter and gonadosomatic index were positively correlated with ovary size. Thus, one of the assumptions of discriminant analysis was not met since variance-covariance matrices were not statistically equal even though data were transformed. The discriminant function was used to score individual females. The Games and Howell test (Sokal and Rohlf, 1981) was then used to contrast groups identified by the discriminant analysis.

Results

Gonadal and morphometric maturity

Fifty percent gonadal maturity occurred at 50.2-mm CL in males and at 60.6-mm CL (95% confidence limits: 58.3–62.9) in females (Fig. 2A). Even though the largest females did not carry eggs, we assumed they were mature because their ovaries were normally developed. The smallest male with spermatophores was 49.1 mm CL, whereas the largest one without spermatophores was 70.2 mm CL. The smallest female carrying eggs was 59.7 mm CL and the largest one without eggs and without developed ovaries was 75.1 mm CL.

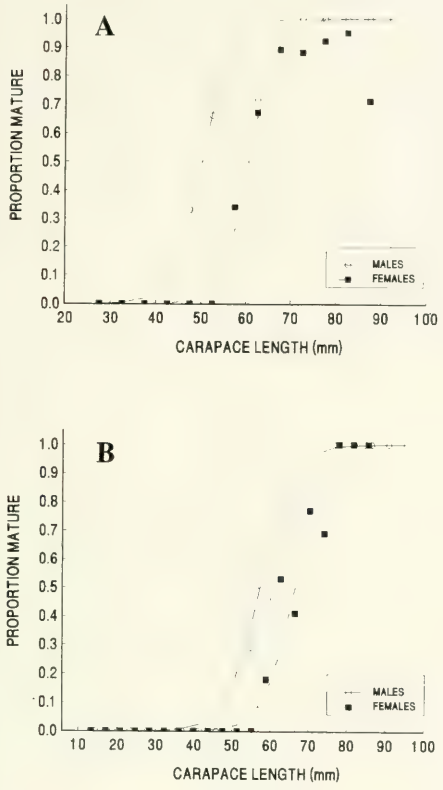

Figure 2

Gonadal and morphometric maturity in *Paralomis granulosa*. Size at 50% maturity is given by the intersection between the calculated logistic function and 0.5 ordinate. (**A**) Proportion of mature *P. granulosa* on the basis of presence of spermatophores in 137 males and presence of eggs or empty egg capsules in 732 females. (**B**) Proportion of mature *P. granulosa* on the basis of allometric growth of chelae.

Size at morphometric maturity was calculated for 851 females (11–88.8 mm CL) and 759 males (6.5–115.1 mm CL). The slope of the regression of chela height on carapace length for juvenile males (<49.1 mm CL; slope=1.012) was significantly less (F=385.7; P<0.001) than that for adult males (>70.2 mm CL; slope=1.473) (Fig. 3). The slope of the regression for known juvenile females (<59.7 mm CL; slope=0.96) was significantly greater (F=223.0; P<0.001) than that of adult females (>75.1 mm CL; slope=0.84). Estimated size at morphometric maturity 50% were 57.0 mm CL (95% confidence limits: 53.9–60.1) for males and 66.5 mm CL (95% confidence limits: 63.4–69.5) for females (Fig. 2B). These results indicated that the method can be applied to both sexes.

Embryogenesis

Embryogenic development was divided into five stages as follows:

Embryonic Stage I (ES I): Spherical or slightly ellipsoidal egg. Yolk bright yellow or orange. A perivitelline space present between the chorionic membrane and the yolk mass. No evidence of division.

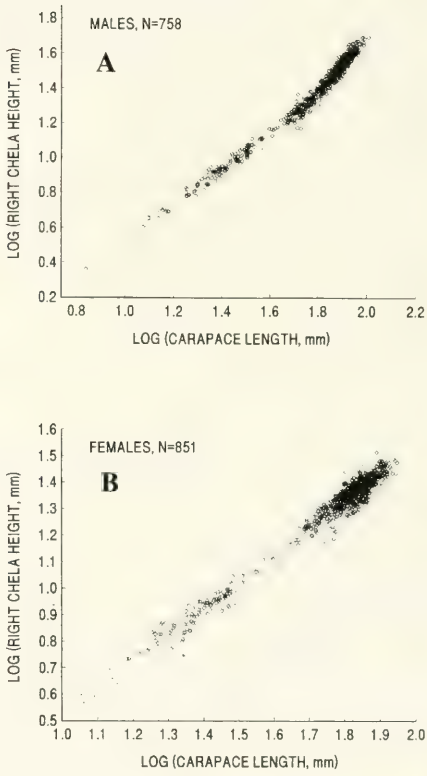

Figure 3

Scattergrams of log right chela height on log carapace length for 758 males (**A**) and 851 females (**B**) of *Paralomis granulosa*. Data for regenerated chelae were removed. Dotted line shows the intersection of juvenile and mature regressions and represents size at maturity: CL = 57 mm for males; CL = 66.5 mm for females.

Embryonic Stage II (ES II): Similar to stage I but a whitish mass of cells visible on yolk surface. This mass is associated with a slight depression in the yolk where the perivitelline space is deeper.

Embryonic Stage III (ES III): A whitish embryo without pigmentation clearly visible, occupying approximately 20% of egg volume. Eye spots clearly outlined. A dorsal organ is present at opposite of embryo (cf. ectodermal thickening of other malacostracan and peracaridan embryos; Anderson, 1982). Abdomen is segmented (5 somites+telson). Telson with 5–7 setae on each of the two lobes. Antennulae and antennae have setae-like projections. Three pairs of appendages are formed posterior to the antennae: mandible, maxillula, and maxilla.

Embryonic Stage IV (ES IV): Egg ellipsoidal; embryo occupies up to 50% of egg volume. Eye spots with ocular pigments. Up to 200 red chromatophores present on carapace. Dorsal organ no longer found.

Embryonic Stage V (ES V): Egg ellipsoidal, pale brown to pale orange. Fully developed zoea clearly visible. Embryo occupying from 50% to almost all of egg volume. Yolk masses reduced and restricted to two dorsal areas in the anterior third of the cephalothorax. All post-mandibular cephalothoracic appendages are differentiated into 3 pairs of maxillipeds and 5 pairs of pereopods, the last one reduced. Telson with 9 setae on each lobe. Heart beat evident.

Duration of embryogenesis and molt stages

Females held in the laboratory were divided into two groups on the basis of embryonic development. One group of females had eggs in ES II from April 1990 up to September 1990 through February 1991, when ES III appeared. ES III did not last longer than two months (in each egg mass) and in May 1991 all eggs were in stage IV. Therefore, these eggs spent autumn and winter in stage II, which suggests an arrest in embryonic development or diapause. The second group of females had clutches with eggs in ES IV in April 1990, which hatched into larvae in October 1990. Post-ovigerous females molted in November 1990, and then extruded and attached eggs in the absence of males. These eggs were unfertile since females have no receptacle to store male gametes (cf. spermathecae in majids). The unfertilized eggs were lost within the next 20 days.

Females collected from the Beagle Channel at any time during the year had egg masses with eggs either in early (I or II) or late (III, IV, or V) stages of development (Table 1; Fig. 4A). ES I and ES II were generally >40% in frequency during the two sampled years. ES III never exceeded 5% in frequency and was observed in February and August 1989, and in April, July, and October 1990. These findings suggest that diapause ends between early winter and late summer, as observed in the laboratory. ES IV and ES V occurred mainly from late autumn to early spring. Post-ovigerous females appeared from late autumn to early spring.

Samples of *P. granulosa* taken from the study area at any given time comprised females in at least two different molt stages: either EIM or AIM occurred with MIM (Table 1, Fig. 4B). PRM females occurred in October and POM females were found in October and November 1989.

Asynchronous embryonic development

A portion of the females (21%; n=100) from the Bécasses Islands, and some from the area near Ushuaia (2%; n=395) carried clutches with eggs at different stages of development: ES II and ES IV or V were found in the same egg mass. This was observed around the Bécasses Islands in August 1990, where 7 females carried eggs in ES II (at least 50% frequency in each clutch) and in ES IV. In October 1990, 12 females had eggs in ES II (at least 50% frequency) and ES V. Two other clutches had eggs in ES II and ES IV. The more advanced eggs would probably hatch earlier than those that were less developed. We could not determine when hatching occurred because commercial fishing around the Bécasses Islands was suspended in October 1990 and the females were not held for further observation.

Table 1

Embryonic development and shell condition of female *Paralomis granulosa* on 20 May 1990 in two localities, 10 km apart. ES=embryonic stages. Postovigerous females have empty egg cases and funiculi attached to the pleopodal setae. MIM=median intermolt; AIM=advanced intermolt. Frequencies for both embryonic development and shell-condition are significantly different between the two localities (G-test for homogeneity on embryonic development = 12.66; P<0.005; G-test for homogeneity on shell condition = 23.45; P<0.005).

	Embryonic development			Shell condition		
Location	ES I, II, and III	ES IV and V	Postovig. females	MIM	AIM	n
Golondrina	60	31	9	64	35	587
Bridges Is.	44	51	5	31	69	84

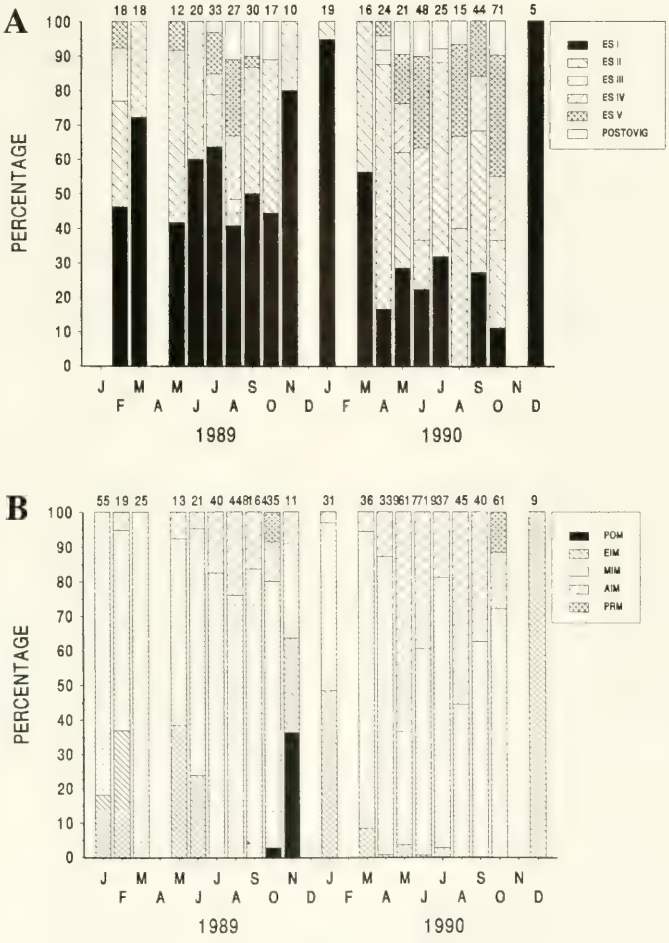

Figure 4

(**A**) Frequency of occurrence of egg stages through two years of sampling. Sample sizes are indicated above bars. Months with no samples are bare. (**B**) Frequency of occurrence of molt stages through two years of sampling. Sample size are indicated above bars. Months with no samples are bare.

Embryonic growth

Eggs from a single clutch increased significantly in size from the ES II (1.71 mm) to ES V (1.96 mm) (paired *t*-test: t=4.604; 3 df; P=0.02) in approximately one year of incubation in the laboratory. Within each asynchronously developing clutch, eggs in ES II (1.87 mm) were significantly smaller than those in ES IV or ES V (1.94 mm) (completely randomized ANOVA; F=22.5; 1,12 df; P<0.001). Egg size at a given stage of development varied significantly among females (F=13.28; 12,12 df; P<0.001). This demonstrates that embryonic growth cannot be generalized from eggs of individual female *P. granulosa*.

Development and maturity of ovaries

Ovarian development of *P. granulosa* was described in detail by Lovrich (1991) and is similar to that of *L. santolla* (Vinuesa, 1984). The only difference with the latter was that oocytes in the ovaries of female *P. granulosa* that had recently molted and spawned were already in an early vitellogenic phase. These oocytes were surrounded by fibrous connective tissue and radiated outwards from the germ strand.

Two groups of females, separated by differences in oocyte diameter (OD) and gonadosomatic index (GSI), were present in virtually all of the sampled months (Figs. 5 and 6). Discriminant analysis on a matrix consisting of CL, CH, OD and GSI (n=220 females sampled during 1990) gave 2 groups. The first included POM, EIM, or MIM females with eggs in ES I and ES II, the second comprised AIM or PRM females with eggs in ES III, ES IV, or ES V. The resulting discriminant function was

$$y = 0.083\ \mathrm{CL} + 0.08\ \mathrm{CH} - 0.727\ \mathrm{OD} - 0.323\ \mathrm{GSI},$$

where coefficients were standardized by the standard deviations within groups. The canonical correlation was 0.798. The reproductive variables OD and GSI dominated the function, whereas morphological measurements contributed negligibly (canonical loadings: CL: 0.17; CH: 0.155; OD: –0.955; GSI: –0.866).

An *a posteriori* classification was generated from the discriminant function. After applying the discriminant function to data for individual females we found that mean scores (i.e., y in function above) were significantly different for each group (Games and Howell test, t'_s=2.49; P<0.01). We thus conclude that there are two distinct groups differing in shell condition and development of ovaries and eggs. These two groups are a key feature of a biennial reproductive cycle.

Females with asynchronous embryonic development were grouped by the discriminant analysis with females in their first year of the reproductive cycle. In fact, for these females, mean GSI was 2.78% in August and 3.38% in October, representing 45 to 55% of maximum GSI (fully developed ovaries in October, Fig. 5), respectively. Their average OD was 1.24 mm in August and 1.36 mm in October, whereas the maximum expected at the end of the reproductive cycle was 1.8 mm (Fig. 6).

Fecundity and reproductive effort

Fecundity was studied in relation to carapace length in the Ushuaia (Fig. 7) and Bécasses Islands. Clutches in late stages (ES IV or ES V) were analyzed separately to avoid underestimations due to possible loss of eggs (Kuris, 1991). Regressions of fecundity on carapace length were significant (Table 2; Fig. 7) and the slopes did not differ between females carrying clutches with eggs in ES I-II, in ES V, or with asynchronously developing eggs (from Bécasses Islands) (F=1.12; P=0.33). ANCOVA indicated that females with ES V eggs or with asynchronously developing eggs had fewer eggs per clutch than those with ES-I and ES-II eggs (F=7.29; P<0.001) (Table 2). Adjusted fecundity was

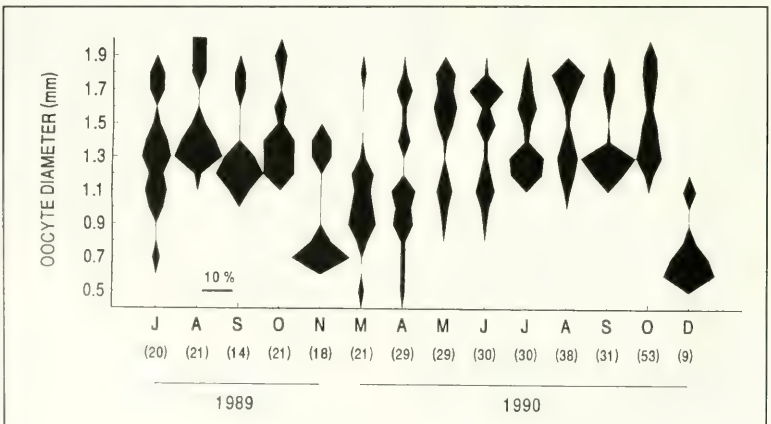

Figure 5

Relative frequency of oocyte diameter for female *Paralomis granulosa* caught in the Beagle Channel. Sample size is indicated in parentheses below each month.

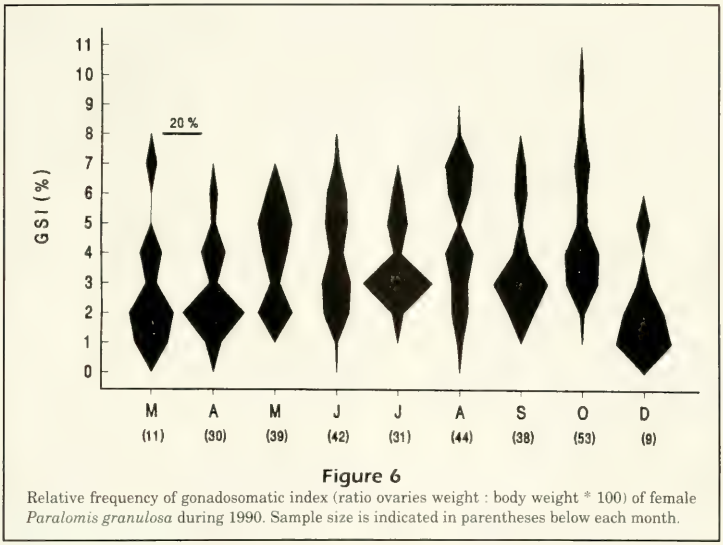

Figure 6

Relative frequency of gonadosomatic index (ratio ovaries weight : body weight * 100) of female *Paralomis granulosa* during 1990. Sample size is indicated in parentheses below each month.

3,688 eggs for females with ES-V eggs and 3,783 eggs for females with asynchronously developing eggs, representing about 88–90% of the estimated 4,201 eggs of females with ES I–II clutches for a constant carapace length (71.0 mm).

The ovaries and clutch of female *P. granulosa* were limited to less than 6–7% of body size. Brood weight varied from 3.67 to 30.39 g and scaled isometrically with weight of body, excluding clutch. Brood weight was at most 7% of female body weight:

log clutch weight = –0.94 + 0.89 log weight (body excluding clutch)

(n=196; r^2= 0.303 $F_{regression}$ = 81.99, P<0.001; t-statistic for H_0 slope=1 = –1.122; P=0.26).

In addition, towards the end of the reproductive cycle in October (23rd month), GSI was about 6–7% (Fig. 6).

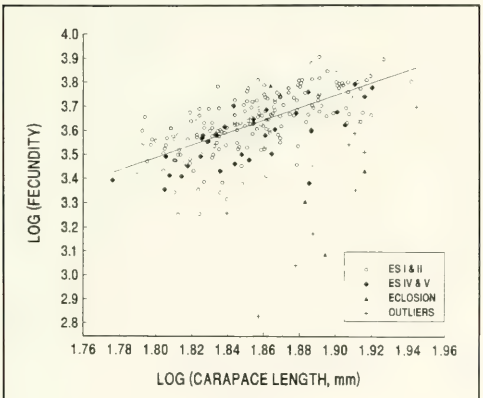

Figure 7

Scattergrams of log fecundity (eggs carried by a female) on log carapace length for *Paralomis granulosa* from Ushuaia area. ES I and II, n=192; ES IV and V, n=32; hatching eggs, n=4; outliers, n=9. The line represents the calculated equation for clutches in ES I and II.

Discussion

Our data indicate that *Paralomis granulosa* has a biennial reproductive cycle. First, female *P. granulosa* molt from late October to November, as evidenced by occurrence of PRM and POM stages (Fig. 4B). We consider that this event marks the beginning of the molt cycle and thus of the reproductive cycle. The frequencies of the different molt stages were consistent with those of the embryonic developmental stages, suggesting that embryogenesis and molting are phased. Embryogenesis lasts 18–22 months and is protracted by a 10-month diapause. Females with ES-I and ES-II eggs were always present throughout the year in the field samples and laboratory. Eggs are extruded from October through November and embryonic development stops or slows at the beginning of cell division (ES II probably representing the diapause stage). After approximately one year of incubation, embryonic development resumes between October and January, and

Table 2

Predictive regression of fecundity (F) on crab size (CL, in mm) in two different locations of the Beagle Channel, during 1989 and 1990. Regressions for different stages of embryonic development (ES) are presented for Ushuaia. R^2=coefficient of determination; F=F-statistic; ***=P<0.001.

Embryo development and location	Equation of regression	n	r^2	F	CL range (mm)
(1) ES I and II (Ushuaia)	$\log F = -1.21 + 2.61 \log CL$	192	0.459	161.3***	60.2–88.0
(2) ES V (Ushuaia)	$\log F = -1.03 + 2.48 \log CL$	32	0.501	33.2***	59.7–83.2
(3) Asynchronous (Bécasses I.)	$\log F = -2.72 + 3.41 \log CL$	43	0.528	45.9***	61.1–78.4

Average log CL = 1.851 (± 0.034)

Adjusted log F (1) = 3.633 (± 0.007)
Adjusted log F (2) = 3.567 (± 0.017)
Adjusted log F (3) = 3.578 (± 0.015)
(1) ≠ (2) & (3), $P < 0.01$; (2) ≠ (3), $P = 0.63$

continues through the next winter, when eclosion occurs. Second, females separated into two groups on the basis of brood development, shell condition, and maturity of ovaries (Table 1; Figs. 5 and 6). In general, females that carried eggs in ES IV and ES V were in advanced molt stages (AIM and PRM) and had fully developed ovaries; by contrast, females with eggs in ES I, ES II, and ES III were in EIM or MIM stages and had small ovaries. Additionally, the presence of oocytes in early vitellogenesis in the recently spawned ovary denotes that oogenesis started before spawning and thus lasts more than two years. In *Lithodes santolla*, oogenesis lasts 24 months (Vinuesa, unpubl. data) while embryogenesis lasts 11 months (Vinuesa, 1984).

The asynchronous embryonic development of *P. granulosa* is a novel feature among lithodid crabs. Our data suggest that some of the eggs within a single clutch develop in 12–14 months and hatch in early summer, while the remainder of the eggs complete their development during the next 10 months. We discount the possibility of a second mating and egg extrusion without molting because 1) there is no seminal receptacle, and chitinous plates cover the gonopores during intermolt, and 2) the ovaries of females with asynchronously developing eggs were in the first year of their cycle. There is clearly a regional effect involved in asynchronous development since females from Ushuaia had more uniformly developed broods. However, with data presently available, we cannot speculate on the causes of this phenomenon.

Since gonadal maturity (presence of gametes) does not necessarily imply morphometric maturity (crabs with differentiated secondary sexual characters), these two terms should be used to define different events in life history that may or may not occur simultaneously. We consider that these concepts are applicable to *P. granulosa* since different sizes at maturity were calculated by using different features (Figs. 2 and 3). Size at maturity for *P. granulosa* tends to increase with increasing latitude (Table 3). This relationship has been noted for *L. santolla* as well (Vinuesa, 1985). By contrast, in the Northern Pacific, size at maturity of lithodid crabs decreases with increasing latitude (Jewett et al., 1985; Somerton and Otto, 1986; Blau, 1990; Otto et al., 1990). Causes of geographical variation in size at maturity are still unknown, but environmental conditions such as bottom temperature may be a factor.

Traps may give biased samples because 1) they select for larger animals (Miller, 1990, but see Blackburn et al., 1990), 2) small crabs and females are excluded

Table 3

Size at maturity (in mm) of *Paralomis granulosa* in different localities. Size at morphometric maturity (SMM) is presented for males and size at gonadal maturity (SGM) for females. Where available, ±95% confidence intervals are presented in parentheses.

Area	Males (SMM)	Females (SGM)
Malvinas I. (Falkland)[1] (51°30'S)	52 (2.15)	46
Seno Otway[2] (53° S)	64	52
Magellan Strait[2] (52°30'S–53°S)	71	62
Beagle Channel (1981–2)[2] (54°55'S)	75	66
Beagle Channel (this study)	57 (3.1)	60.6 (2.3)

[1]Hoggarth, D.D., National Rivers Authority, Welsh Region, Gwyneedd, UK, pers. commun. 1992.
[2]Campodónico et al. 1983.

by larger males, and 3) crabs near ecdysis and berried females are less vulnerable to trapping since they do not feed (Miller, 1990). Size at maturity of *P. granulosa* may be overestimated because the 57.5-mm-CL size class was poorly sampled; this would particularly affect size at gonadal maturity. Also, the frequency of occurrence of females with late embryonic stages, especially those in pre- and postmolt conditions, may be underestimated by trap sampling. Unfortunately, we have no way to assess these possible biases because we have no trawl surveys with which to compare data.

Compared with other shallow-dwelling lithodids, *P. granulosa* has low fecundity and large eggs, resembling in this respect the deep-water species: *Lithodes ferox* (8,000 eggs maximum, 1.97 mm egg diameter; Abelló and Macpherson, 1992); *L. couesi* (5,000, 2.3 mm; Somerton, 1981); *L. murrayi* (4,200, 2.45 mm; Miquel and Arnaud, 1987; Miquel et al., 1985). By contrast, the shallow water *Paralithodes camtschaticus* and *P. platypus* carry up to 350,000 and 280,000 eggs, respectively, with an average egg diameter of 1.2 mm (Matsuura et al., 1971, 1972; Somerton and MacIntosh, 1985). Fecundity of *P. granulosa* was less in females with ES V or with asynchronously developing clutches for a constant carapace length (Table 2), because of egg loss. At the end of embryogenesis about 10–12% of the initial brood was lost. Diseases and egg predators are frequent causes of egg loss in crab species (Kuris, 1991). However we did not find evidence of epibiosis in broods of *P. granulosa*. Exceptionally small broods, outliers in Fig. 7, may have resulted from delayed mating, lack of mates, or to small size of mating males, as occurs in other lithodids (McMullen, 1969; Powell et al., 1973; Paul and Paul, 1990). This question requires further investigation.

As the energy expended on each offspring increases, the number of offspring that parents produce decreases (Smith and Fretwell, 1974). Thus, in two related species similar energetic investment may result in many small or few large offspring. However, considering the two lithodids of the Beagle Channel, one finds that *P. granulosa* biennially produces eggs which are fewer but not larger than those of *L. santolla*, which annually produces up to 59,000 eggs (Guzmán and Campodónico, 1972) of 2.1–2.2 mm in diameter (Vinuesa, 1987).

There is no evidence that the biennial reproductive cycle of *P. granulosa* is more advantageous (i.e., an adaptative strategy) than the annual cycle of *L. santolla*. *Paralomis granulosa* larvae pass through fewer molting events (Campodónico, 1971; Campodónico and Guzmán, 1981); thus mortality due to ecdysis is reduced. Shorter larval development would also reduce predation risks in the plankton. Inhabiting the layer of water closest to bottom (Lovrich, unpubl. data) allows larvae to find refuge and thus reduces losses to predation. We speculate that the lesser fecundity of *P. granulosa* may be partially compensated for by a high survival during their development. In *Paralithodes platypus*, Jensen and Armstrong (1989) interpreted biennial reproduction as a consequence of physiological and energetic constraints incurred by the species in a harsh environment.

King crab species can be categorized into three groups on the basis of their reproductive cycles: *Paralithodes camtschaticus* and *Lithodes santolla* spawn annually, *Paralomis granulosa* and *Paralithodes platypus* (except primiparous females) spawn biennially, and finally *L. aequispina, L. couesi*, and *L. ferox* spawn asynchronously. All *Lithodes* species, with the exception of *L. santolla*, inhabit deep waters whereas *Paralithodes* species inhabit shallow waters. Otto and Cummiskey (1985) hypothesized that king crabs inhabiting shallow waters (*L. santolla, P. camtschaticus,* and *P. platypus*) spawn synchronously during spring while deep-sea king crabs (*L. aequispina* and *L. couesi*) have protracted spawning periods. These authors suggest that this pattern could be related to a dependence on food sources by shallow water species. *Paralomis granulosa* inhabits shallow waters and spawns synchronously every two years, but we suppose that in this species synchronicity is not related to food dependence because larval hatching occurs mainly during winter when neither food nor potential competitors are abundant (Lovrich, unpubl. data).

Paralomis is a deep-water genus (Takeda et al. 1984; Macpherson, 1988) and *P. granulosa* is the only species that inhabits shallow waters. This species probably colonized the Beagle Channel relatively recently, i.e., 8,500 years ago after the last deglaciation occurred (Rabassa et al., 1986). This species still retains certain features of its deep-water relatives: low fecundity, large eggs, protracted reproductive cycle, and independence of larval hatching from food availability.

Acknowledgments

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The assumption of constant selectivity and the stock assessment for widow rockfish, *Sebastes entomelas*

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Abstract.—Modern methods for fish stock assessment are often based on age-structured models that separate each coefficient of fishing mortality at age into a time-specific factor (the rate of fishing mortality on the fully exploited age-classes) and an age-specific factor (a selectivity coefficient that measures the relative vulnerability of the particular age-class). The assumption that the selectivity coefficients are constant through time greatly simplifies the assessment process because it allows for a reduction in the number of unknown parameters. However, if the assumption is incorrect, it can lead to incorrect estimates of stock status.

The most recent stock assessment for Pacific widow rockfish (*Sebastes entomelas*) was based on the untested assumption that the selectivity coefficients have not changed over the years. This assessment was derived from an analysis of catch-at-age data by using an assessment method known as the Stock Synthesis program. The work described here examined the sensitivity of the assessment results to the assumption of constant selectivity. Simulation experiments with the Stock Synthesis program showed that the stock size estimates for widow rockfish can be highly sensitive to modest changes in selectivity. Experiments with two other assessment techniques, which also assume constant selectivity (the CAGEAN program of Deriso, Quinn, and Neal and the multiplicative catch-at-age model of Shepherd and Nicholson), showed that these methods are similarly sensitive to changes in selectivity.

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In general, individual fish in a stock are not equally likely to be caught and different age-classes of fish do not experience identical rates of fishing mortality. In the fisheries literature this phenomenon is usually described as "selectivity" or "availability" or "partial recruitment" (Megrey, 1989). In some instances selectivity results from the physical properties of the fishing gear. For example, younger and smaller fish may pass unharmed through the meshes of a trawl, whereas older and larger individuals may sense and avoid an approaching net. Alternatively, selectivity can result when different age-classes of fish occupy geographic regions that are not fished with the same intensity. If younger fish are offshore and older ones are inshore, for example, then the age distribution of fish in the catch will depend not just on the stock's age distribution but also on the fishing locations. Selectivity coefficients, which measure the relative influence of fishing on the age structure of the stock, are fundamental parameters in the analysis of catch-at-age data.

Many stock assessment procedures attempt to reconcile observations of catch-at-age with an underlying age-structured population model and thereby reconstruct the demographic history of the stock (Megrey, 1989). If different age-classes experience the same relative susceptibility to fishing each year, then one can model each annual age-specific rate of fishing mortality as the simple product ($S_a \cdot F_y$) of an age effect (the selectivity coefficient, S_a) and a year effect (the fishing mortality coefficient, F_y). Because there are an infinite number of (S_a, F_y) pairs that correspond to a given age-specific rate of fishing mortality, the selectivity coefficient for at least one age class must be assumed constant. If the largest S_a is set equal to one, then the F_y values correspond to the rate of fishing mortality on the fully exploited age classes.

Formulating the fishing mortality coefficient as the product of a year-effect and an age-effect greatly simplifies an analysis of catch-at-age data because it reduces the number of essential parameters. For example, if the catch-at-age matrix contains data for A ages and Y years, and if the selectivity coefficients are constant for all years, then there are only $(A+Y)$ unknown parameters. However, if the selectivity coefficients change every year, then there are $(A \cdot Y)$ unknown parameters.

Constant selectivity, and the consequent separability of fishing mortality into age and year effects, is a fundamental assumption for numerous stock assessment procedures, including separable Virtual Population Analysis (Pope and Shepherd, 1982), the CAGEAN program (Deriso et al., 1985, 1989), the multiplicative model of Shepherd and Nicholson (1986, 1991), and the Stock Synthesis program (Methot 1989, 1990). Fish stocks that have recently been as-

sessed by using one or more of these procedures include Pacific halibut (*Hippoglossus stenolepis*) in the northeast Pacific (IPHC, 1991), walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska (Megrey, 1991), Dover sole (*Microstomus pacificus*) along the U.S. west coast (Turnock and Methot, 1991), and scad (*Trachurus trachurus*) from Atlantic waters off Spain and Portugal (Borges, 1990).

Despite the widespread application of assessment methods that are based on the notion that selectivity is time-invariant, I know of no published studies that examine the sensitivity of these assessment procedures to violations of the constant selectivity assumption. It appears that often these assessment methods are applied without first verifying that selectivity was constant for the stock being assessed. Gudmundsson (1986) recommended extensive analysis to avoid mis-specifying the catch-at-age model (for example, incorrectly assuming that selectivity was constant), and he developed a least-squares technique for testing the separability assumption. However, his methodology does not seem to be used widely.

Several published papers document variations in selectivity through time. Houghton and Flatman (1981) examined selectivity coefficients for cod (*Gadus morhua*) in the west-central North Sea and found significant changes in the "exploitation pattern," which they attributed to shifts in the fishing pressure exerted by different segments of the fleet. Gudmundsson (1986) speculated that changes in fish size-at-age coupled with variations in the composition of the fishing gear caused changes in selectivity for the Icelandic stock of cod (*Gadus morhua*). Gordoa and Hightower (1991) analyzed data from the fishery for Cape hake (*Merluccius capensis*) off southwestern Africa and ascribed significant shifts in selectivity to the fishermen's targeting on strong year classes.

The work described here has a different focus. In this paper I do not examine how selectivity in a fishery has varied. Instead, I investigate whether the stock assessment program used to evaluate a particular stock's status is robust to changes in selectivity. For this exercise I analyzed the stock assessment for widow rockfish (*Sebastes entomelas*), an economically important component of the complex of Sebastes species found along the Pacific coast of North America. Gunderson (1984) described the history and characteristics of the U.S. fishery for widow rockfish off the coasts of Washington, Oregon, and California.

In this paper, I demonstrate that the stock size estimates for widow rockfish, which are based on the untested assumption that selectivity has been constant from year to year, can be seriously biased if the assumption is violated. Furthermore, I test two other assessment methods that also use the constant selectivity assumption and show that they produce similarly biased results. Finally, I establish that comparable problems with bias can arise in the assessment results for other fish stocks, whose biological characteristics differ significantly from widow rockfish.

Methods

One technique for testing the reliability of an estimation procedure is to produce artificial data sets with known characteristics and then to estimate the parameter values from which the data were derived. I used this approach to determine whether certain stock assessment methods were sensitive to violations of the constant selectivity assumption. First, I simulated catch-at-age data for a fish stock in which the selectivity coefficients were changing slowly from year to year. Next, I used the assessment programs to analyze the catch-at-age data and to estimate stock biomass and abundance-at-age. Finally, I measured the bias of the estimates by calculating the relative errors of the estimates. The relative error of an estimate is the difference between the estimate and its true value; all divided by the true value.

Sensitivity of the Stock Synthesis program when applied to data for widow rockfish

To investigate the sensitivity of the stock assessment results for widow rockfish to the assumption of constant selectivity, I developed a spreadsheet model to generate artificial catch-at-age data, which I then analyzed using the Stock Synthesis program. The Stock Synthesis program has been used by the Pacific Fisheries Management Council (PFMC) since 1990 to appraise the status of many of the Pacific groundfish stocks (PFMC, 1990). Methot (1989, 1990) documented the principles and equations underlying the Stock Synthesis program.

The spreadsheet model simulates the characteristics of an age-structured population and employs the same equations as the Stock Synthesis program for describing the temporal progressions in abundance-at-age, biomass, catch-at-age, and total catch. The model uses parameters for mortality and growth that are similar to those observed in the U.S. stock of widow rockfish (Table 1). I generated values for abundance-at-age and catch-at-age for 10 years and 20 age classes, ages 4 through 22, as well as age 23 and older (Table 2). In 1989, almost 95% of the U.S. coast-wide landings of widow rockfish were fish between the ages of 5–10 years; about 3% of the landings were fish older than 15 years (Hightower and Lenarz, 1990).

Table 1

Parameters for simulating a stock of widow rockfish: annual recruitment was 10^6 fish per year; natural mortality[1] was 0.15 per year. Selectivity parameters[2] (Curve B (Fig. 1), 100% selection at age 8): lower inflection age was 6.0 years; lower slope was 2.5 per year; upper inflection age was 12.0 years; and the upper slope was 0.3 per year.

Age (years)	Selectivity coefficients (%)	Weight[3] (kg)
4	0.8	0.549
5	8.9	0.662
6	56.2	0.780
7	99.0	0.936
8	100.0	1.025
9	93.1	1.150
10	84.6	1.255
11	75.2	1.400
12	65.5	1.427
13	55.7	1.596
14	46.4	1.798
15	37.9	1.899
16	30.3	1.965
17	23.9	1.965
18	18.6	2.008
19	14.3	2.099
20	10.9	2.031
21	8.2	2.704
22	6.2	2.299
23+	4.7	2.388

[1]From Hightower and Lenarz (1990).
[2]The equation for the double-logistic selection curve and the meaning of these parameters are described in Methot (1990).
[3]From Barss and Echeverria (1987).

In the first set of experiments, I examined combinations of three factors to determine how they affect bias in the estimates from the Stock Synthesis program. They were 1) the age of full selection was either gradually increasing or decreasing from year to year, or it varied randomly; 2) the annual fishing mortality coefficients were either increasing, decreasing, or constant; and 3) the program was either given the true values of annual recruitment or it was required to estimate these values. For simplicity, I limited my experiments to these three factors, although undoubtedly there are others that can also have significant effects. Examples are trends in annual recruitment, the level of natural mortality, or the shape of the selectivity curve.

True values for the selectivity coefficients were generated from a double logistic function (Methot, 1990) and were similar to those reported for widow rockfish in Hightower and Lenarz (1990). The strongly domed shape of the selectivity curve (Fig. 1), which may be due to the movement of older individuals into deeper, less heavily fished waters, seems to be a common feature for many of the groundfish stocks in the U.S. Pacific Northwest.

To simulate temporal changes in selectivity, I shifted the selectivity coefficients forward or backward by one age class (Fig. 1). When selectivity increased, 100% selection occurred at age 7 for the first three years (Curve A), at age 8 for the next four years (Curve B), and at age 9 for the last three years (Curve C). When selectivity decreased, full selection occurred at age 9 for the first three years, at age 8 for the next four years, and at age 7 for the last three years. To measure the effects of "random" changes in selectivity, I generated data sets for 10 trials. Selectivity in the first year of each trial always followed selection curve B, but the sequence of curves that applied in the subsequent years came from a random shuffling of the sequence AAABBBCCC (Fig. 2). Curve A applied in three randomly chosen years, curve B applied in three other randomly selected years, and curve C applied in the remaining three years. I did not examine other forms of change in selectivity, such as variation in the basic shape of the curve.

When simulating an increasing trend in fishing mortality, the fishing mortality coefficients changed linearly from 0.10 to 0.28 per year, at increments of 0.02 per year. When the trend was decreasing, the fishing mortality coefficients varied from 0.28 to 0.10 per year, at increments of –0.02 per year. When there was no trend in fishing mortality, the fishing mortality was 0.20 per year, which is approximately the rate of fishing that reduces the reproductive output from this simulated stock to 35% of its unexploited level when full selection is at age 8 years (Fig. 1, Curve B).

All methods for analyzing catch-at-age data require additional information with which to tune the analysis and thereby resolve a basic indeterminacy in the model for catch[1] (Shepherd and Nicholson, 1986). In the most recent assessment for widow rockfish, Hightower and Lenarz (1990) tuned the Stock Synthesis analysis to a single fishing mortality coefficient, but in many contemporary assessments of other Pacific groundfish stocks the Stock Synthesis runs have been tuned to estimates of abundance-at-age or biomass from research vessel surveys. In the sensitivity analysis, I gave the Stock Synthesis program auxiliary data for tuning either in the form of the true annual fishing mortality coefficients or the true proportions-at-age.

Sensitivity of other stock assessment programs that assume constant selectivity

To confirm that the assumption of constant selectivity, rather than some unique feature of the Stock Synthesis program, was responsible for any bias in the results, I experimented with two other

[1]Catch-at-age is approximately equal to the product of stock abundance-at-age and fishing mortality-at-age. If only catch data are available, one cannot distinguish between a case of large abundance and low fishing mortality versus one of small abundance and high fishing mortality.

Table 2

Simulated widow rockfish abundance and catch data. (**A**) Selectivity increasing, fishing mortality constant (0.20 year). (**B**) Selectivity decreasing, fishing mortality constant (0.20/year). Selection curves are indicted in parentheses.

A	Year									
Age	1981 (A)	1982 (A)	1983 (A)	1984 (B)	1985 (B)	1986 (B)	1987 (B)	1988 (C)	1989 (C)	1990 (C)
Initial population size (1000s of fish)										
4	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0
5	845.6	845.6	845.6	845.6	859.3	859.3	859.3	859.3	860.6	860.6
6	650.4	650.4	650.4	650.4	715.0	726.6	726.6	726.6	738.4	739.5
7	459.3	459.3	459.3	459.3	500.3	550.0	558.9	558.9	614.5	624.4
8	323.7	323.7	323.7	323.7	324.3	353.3	388.4	394.7	429.9	472.6
9	231.3	231.3	231.3	231.3	228.1	228.5	249.0	273.7	278.7	303.6
10	168.1	168.1	168.1	168.1	165.2	163.0	163.3	177.9	192.9	196.4
11	124.4	124.4	124.4	124.4	122.1	120.1	118.4	118.7	127.1	137.8
12	94.0	94.0	94.0	94.0	92.1	90.4	88.9	87.7	86.3	92.4
13	72.3	72.3	72.3	72.3	70.9	69.6	68.3	67.1	64.9	63.9
14	56.7	56.7	56.7	56.7	55.7	54.6	53.6	52.6	50.7	49.0
15	45.3	45.3	45.3	45.3	44.5	43.7	42.8	42.0	40.5	39.0
16	36.7	36.7	36.7	36.7	36.1	35.5	34.9	34.2	33.0	31.8
17	30.1	30.1	30.1	30.1	29.7	29.3	28.8	28.2	27.3	26.3
18	25.0	25.0	25.0	25.0	24.7	24.4	24.0	23.6	22.9	22.1
19	20.9	20.9	20.9	20.9	20.7	20.5	20.2	19.9	19.4	18.8
20	17.6	17.6	17.6	17.6	17.5	17.3	17.1	16.9	16.5	16.1
21	14.9	14.9	14.9	14.9	14.8	14.7	14.6	14.4	14.1	13.8
22	12.7	12.7	12.7	12.7	12.6	12.5	12.5	12.3	12.1	11.9
23+	74.3	74.3	74.3	74.3	74.1	73.9	73.7	73.4	72.8	72.2
Catch (1000s of fish)										
4	16.30	16.30	16.30	1.49	1.49	1.49	1.49	0.13	0.13	0.13
5	83.61	83.61	83.61	13.78	14.01	14.01	14.01	1.28	1.28	1.28
6	108.74	108.74	108.74	64.31	70.70	71.85	71.85	11.85	12.04	12.06
7	77.51	77.51	77.51	76.78	83.64	91.95	93.44	55.26	60.75	61.74
8	51.17	51.17	51.17	54.62	54.73	59.62	65.54	65.98	71.88	79.02
9	33.49	33.49	33.49	36.56	36.06	36.13	39.36	46.18	47.03	51.23
10	21.85	21.85	21.85	24.34	23.93	23.60	23.65	28.12	30.49	31.05
11	14.21	14.21	14.21	16.18	15.88	15.61	15.40	17.19	18.41	19.96
12	9.22	9.22	9.22	10.73	10.52	10.33	10.15	11.40	11.21	12.01
13	5.96	5.96	5.96	7.10	6.96	6.83	6.70	7.67	7.42	7.29
14	3.85	3.85	3.85	4.68	4.59	4.50	4.41	5.16	4.97	4.81
15	2.48	2.48	2.48	3.07	3.02	2.96	2.90	3.46	3.34	3.22
16	1.59	1.59	1.59	2.01	1.98	1.94	1.91	2.32	2.23	2.15
17	1.02	1.02	1.02	1.31	1.29	1.27	1.25	1.54	1.49	1.44
18	0.65	0.65	0.65	0.85	0.84	0.83	0.81	1.02	0.99	0.96
19	0.42	0.42	0.42	0.55	0.54	0.54	0.53	0.67	0.66	0.64
20	0.27	0.27	0.27	0.35	0.35	0.35	0.34	0.44	0.43	0.42
21	0.17	0.17	0.17	0.23	0.23	0.22	0.22	0.29	0.28	0.28
22	0.11	0.11	0.11	0.15	0.14	0.14	0.14	0.19	0.18	0.18
23+	0.48	0.48	0.48	0.64	0.64	0.64	0.63	0.84	0.84	0.83

Table 2 (Continued)

B	Year									
Age	1981 (C)	1982 (C)	1983 (C)	1984 (B)	1985 (B)	1986 (B)	1987 (B)	1988 (A)	1989 (A)	1990 (A)
Initial population size (1000s of fish)										
4	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0	1000.0
5	860.6	860.6	860.6	860.6	859.3	859.3	859.3	859.3	845.6	845.6
6	739.5	739.5	739.5	739.5	727.7	726.6	726.6	726.6	661.0	650.4
7	625.3	625.3	625.3	625.3	568.8	559.8	558.9	558.9	513.1	466.7
8	481.0	481.0	481.0	481.0	441.6	401.7	395.3	394.7	393.9	361.6
9	339.7	339.7	339.7	339.7	339.0	311.2	283.1	278.5	282.0	281.4
10	239.4	239.4	239.4	239.4	242.7	242.2	222.3	202.2	202.4	205.0
11	171.0	171.0	171.0	171.0	174.0	176.4	176.0	161.6	149.8	149.9
12	124.3	124.3	124.3	124.3	126.6	128.8	130.6	130.3	122.0	113.1
13	92.0	92.0	92.0	92.0	93.8	95.6	97.3	98.6	100.3	93.9
14	69.5	69.5	69.5	69.5	70.9	72.3	73.6	74.9	77.3	78.7
15	53.5	53.5	53.5	53.5	54.5	55.6	56.7	57.7	59.7	61.7
16	42.0	42.0	42.0	42.0	42.7	43.5	44.3	45.2	46.8	48.4
17	33.5	33.5	33.5	33.5	34.0	34.6	35.2	35.9	37.1	38.4
18	27.1	27.1	27.1	27.1	27.5	27.9	28.4	28.9	29.8	30.8
19	22.3	22.3	22.3	22.3	22.5	22.8	23.1	23.5	24.2	24.9
20	18.5	18.5	18.5	18.5	18.6	18.8	19.1	19.3	19.8	20.4
21	15.4	15.4	15.4	15.4	15.5	15.7	15.8	16.1	16.4	16.8
22	13.0	13.0	13.0	13.0	13.1	13.2	13.3	13.4	13.6	13.9
23+	73.4	73.4	73.4	73.4	73.7	73.9	74.2	74.6	75.2	75.9
Catch (1000s of fish)										
4	0.13	0.13	0.13	1.49	1.49	1.49	1.49	16.30	16.30	16.30
5	1.28	1.28	1.28	14.03	14.01	14.01	14.01	84.97	83.61	83.61
6	12.06	12.06	12.06	73.12	71.95	71.85	71.85	121.48	110.50	108.74
7	61.83	61.83	61.83	104.55	95.10	93.58	93.44	94.32	86.59	78.76
8	80.42	80.42	80.42	81.17	74.52	67.78	66.70	62.40	62.27	57.17
9	57.32	57.32	57.32	53.70	53.59	49.20	44.75	40.34	40.84	40.75
10	37.84	37.84	37.84	34.66	35.14	35.07	32.20	26.29	26.31	26.64
11	24.77	24.77	24.77	22.23	22.61	22.93	22.88	18.45	17.10	17.12
12	16.16	16.16	16.16	14.19	14.46	14.71	14.91	12.79	11.97	11.09
13	10.51	10.51	10.51	9.03	9.21	9.38	9.54	8.13	8.27	7.74
14	6.82	6.82	6.82	5.73	5.84	5.96	6.07	5.08	5.24	5.34
15	4.41	4.41	4.41	3.63	3.69	3.77	3.84	3.16	3.27	3.37
16	2.84	2.84	2.84	2.29	2.33	2.38	2.43	1.96	2.03	2.10
17	1.83	1.83	1.83	1.45	1.47	1.50	1.53	1.22	1.26	1.30
18	1.18	1.18	1.18	0.92	0.93	0.95	0.96	0.76	0.78	0.81
19	0.75	0.75	0.75	0.58	0.59	0.60	0.61	0.47	0.48	0.50
20	0.48	0.48	0.48	0.37	0.37	0.38	0.38	0.29	0.30	0.31
21	0.31	0.31	0.31	0.23	0.24	0.24	0.24	0.18	0.19	0.19
22	0.20	0.20	0.20	0.15	0.15	0.15	0.15	0.12	0.12	0.12
23+	0.84	0.84	0.84	0.63	0.63	0.64	0.64	0.48	0.48	0.49

assessment methods that also use the assumption of constant selectivity. I analyzed the simulated catch-at-age data with the CAGEAN program (CAGEAN-PC, version 4, release 2) of Deriso et al. (1985, 1989) and with the multiplicative catch-at-age model of Shepherd and Nicholson (1986, 1991).

The Stock Synthesis program and the CAGEAN program use similar approaches for modeling catch-at-age, but they differ in their assumptions about variability in the observed data. Stock Synthesis assumes a multinomial error structure for the catch-at-age data. If $\hat{p}_a$ is the predicted proportion of age class (a) captured, then the variance associated with a random observation of p_a is proportional to $\hat{p}_a \cdot (1-\hat{p}_a)$. CAGEAN, however, assumes a lognormal error structure. If $\hat{c}_a$ is the predicted number of fish caught of age class (a), then $\log_e(c_a/\hat{c}_a)$ is normally distributed with a zero mean and a constant variance.

The multiplicative catch-at-age model is essentially an approximation to the catch model that underlies

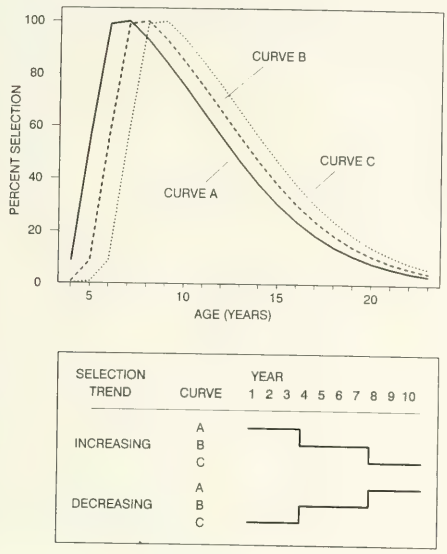

Figure 1

Selectivity curves used in the simulations. To simulate the effects of changing selectivity, the selectivity curve was either shifted towards older fish through time (increasing selectivity) or towards younger fish (decreasing selectivity).

both the Stock Synthesis and CAGEAN programs. Unlike the other two assessment procedures, the multiplicative model estimates relative, rather than absolute, abundance. To conduct the multiplicative catch-at-age analyses, I used the GLIM statistical program (Baker and Nelder, 1985) and assumed a log-normal error structure.

In the experiments with CAGEAN and the multiplicative catch-at-age model, I used a subset of the data from the earlier experiments with the Stock Synthesis program. Two sets of catch-at-age data were analyzed, one from a population with selectivity shifting to older ages (selectivity increasing) and fishing mortality constant (Table 2A), the other from a population with selectivity shifting to younger ages (selectivity decreasing) and fishing mortality constant (Table 2B). I tuned the CAGEAN program to the true fishing mortality coefficients, and constrained the multiplicative catch-at-age analysis to have a trend of zero in the annual fishing mortality coefficients. The experiments here correspond to the cases examined earlier in which the Stock Synthesis program was tuned to fishing mortality and recruitment was estimated.

Sensitivity of the Stock Synthesis program when applied to data from a heavily exploited stock

To determine whether the results from the experiments with a simulated stock of widow rockfish would apply to fish stocks with different biological characteristics, I generated two additional data sets, one from a population with selectivity shifting to older ages (selectivity increasing), the other from a population with selectivity shifting to younger ages (selectivity decreasing). Both simulated populations, which suffered an instantaneous natural mortality rate of 0.30 per year and an instantaneous fishing mortality rate of 0.60 per year, had significantly fewer old animals compared to the populations in the previous simulations. I analyzed the two data sets with the Stock Synthesis program, with tuning to the true fishing mortality coefficients, and with recruitment estimated.

Results

The assessment programs that I investigated all produce a wide variety of estimates, including selectivity coefficients and matrices of abundance and catch by age and year. Rather than evaluating bias for all estimates, my analysis focussed on estimates of annual stock biomass, numerical abundance, and recruitment. Of special importance to a stock assessment scientist or fishery manager is the bias in the estimate of average biomass for the final year of a data series. This estimate is approximately the biomass estimate on which the catch quota for the next year is based[2]. If the estimate of average biomass in the final year is, say, 20% too high, then the quota will be roughly 20% too high; if the estimate is 10% too low, the quota will also be about 10% too low.

Selectivity of the Stock Synthesis program when applied to data for widow rockfish

The results of the experiments with the Stock Synthesis program and the data for the simulated stock of widow rockfish suggest that some of the assessment results can be highly sensitive to slight trends in selectivity. For example, when selectivity shifted towards younger ages, the biomass estimate for the final year of the series was 74% too high (Table 3A; selectivity decreasing, tuned to fishing mortality, fishing mortal-

[2]The annual catch quota is derived from an estimate of the biomass at the end of the previous year, plus an appropriate amount for the new recruitment. In practice this differs little from the estimate of average biomass in the final year.

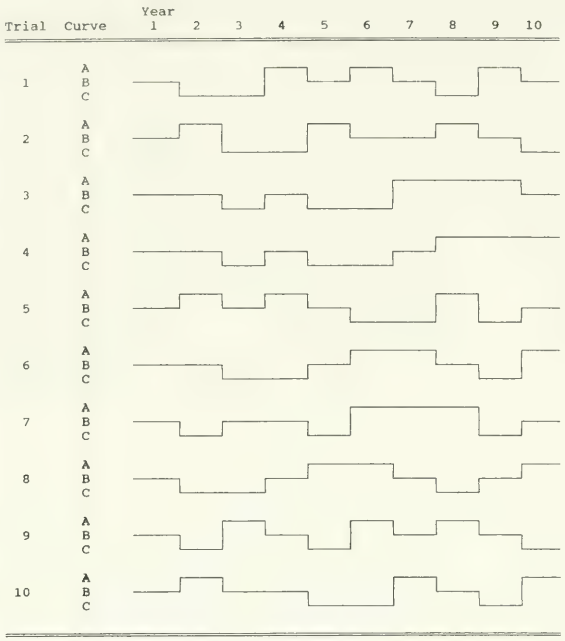

Figure 2

Simulations with random variation in selectivity. The effects of random variation in selectivity were simulated by shuffling the sequence of selectivity curves (AAABBBCCC, Fig. 1) that applied in each of the nine years after the first. The ten sequences shown here were used.

ity constant, and recruitment estimated), and the estimated age distribution in the final year was grossly incorrect (Fig. 3A). The estimated numbers of five-year-old to seven-year-old fish were much too high and the numbers of fish 15 years and older were all slightly too high. When selectivity shifted towards older ages, the biomass estimate for the final year was as much as 59% too low (Table 3A; selectivity increasing, tuned to fishing mortality, fishing mortality increasing, and recruitment estimated) and the program underestimated the numbers of very young and very old fish (Fig. 3B).

In these experiments, bias in a particular estimate was not a simple linear function of the factors examined, but instead involved complicated interactions between factors. Nevertheless, some general effects seemed to apply. When the Stock Synthesis program was tuned to fishing mortality and used to estimate recruitment, shifts in selectivity towards older ages (selectivity increasing) always induced negative bias in the estimates of average biomass, and shifts in selectivity towards younger ages (selectivity decreasing) always induced positive bias (Table 3, A and B). When the recruitment values were known or tuning to the proportion-at-age data was used, however, trends in selectivity had no consistent effect on the direction of bias. Estimation of recruitment values, often, but not always, increased the magnitude of the bias in the estimates of biomass (Table 3, A and B) and abundance (Table 3C). Tuning to proportion-at-age data, instead of to annual fishing mortality coefficients, often decreased the amount of bias in the estimates of biomass, abundance, and recruitment. Bias in these estimates usually was smallest when the trend in fishing mortality was increasing and largest when the trend in fishing mortality was decreasing.

When the Stock Synthesis program estimated recruitment, improvements in the fit were observed relative to those obtained when recruitment values were known (Table 3D). To the assessment scientist interpreting these results, the improved fit would suggest that the program had provided better estimates, when, in fact, the estimates were more biased and less reliable. When selectivity shifted toward older fish, there was a systematic change from year to year in the catch-at-age data, which the program attempted to match by imposing a decreasing trend in recruitment (Fig. 4). When selectivity shifted towards younger fish, the program imposed an increasing trend in recruitment. Similar distortions occurred when the program was tuned to the true proportion-at-age data. This last result suggests that using age-frequency data from research vessel surveys will not eliminate the bias induced by changes in selectivity, even though survey data may not be subject to the changes in selectivity that the fishery might experience.

When selectivity varied randomly (Table 4), the magnitude of the bias in the estimate of the final year's average biomass was usually less than what occurred when selectivity had a trend (Table 3A), but the general patterns seen in the earlier experiments remained.

Table 3

Sensitivity analysis of the Stock Synthesis program. (**A**) Bias[1] in the estimated average biomass in the final year. (**B**) Average and standard deviation[2] of the bias in the estimates of annual average biomass. (**C**) Average and standard deviation of the bias in the estimates of annual numerical abundance. (**D**) Average and standard deviation of the bias in the estimates of annual recruitment[3] and the improvement in fit[4] when recruitment was estimated.

A

	Increasing selectivity		Decreasing selectivity	
	Known recruitment %	Estimated recruitment %	Known recruitment %	Estimated recruitment %
Tuned to fishing mortality				
F increasing	−1.0	−58.8	−1.2	49.8
F decreasing	16.9	−54.4	13.6	72.0
F constant	12.1	−54.0	10.4	74.3
Tuned to proportion-at-age				
F increasing	3.4	−26.1	−2.9	1.0
F decreasing	23.3	−24.6	11.7	5.7
F constant	17.3	−14.0	7.4	5.2

B

	Increasing selectivity				Decreasing selectivity			
	Known recruitment		Estimated recruitment		Known recruitment		Estimated recruitment	
	Mean (%)	SD (%)	Mean (%)	SD (%)	Mean (%)	SD (%)	Mean (%)	SD (%)
Tuned to fishing mortality								
F increasing	3.9	2.1	−32.5	12.7	−4.5	1.3	24.6	16.2
F decreasing	46.0	21.6	−20.8	18.2	21.4	8.0	63.3	18.8
F constant	29.5	11.5	−20.5	17.0	11.8	4.0	53.2	18.2
Tuned to proportion-at-age								
F increasing	4.5	0.5	−12.1	8.4	−3.8	0.4	−6.3	6.9
F decreasing	51.7	20.2	7.6	20.5	24.9	9.6	9.1	11.0
F constant	32.0	10.0	10.8	15.2	13.7	4.9	4.3	7.9

C

	Increasing selectivity				Decreasing selectivity			
	Known recruitment		Estimated recruitment		Known recruitment		Estimated recruitment	
	Mean (%)	SD (%)	Mean (%)	SD (%)	Mean (%)	SD (%)	Mean (%)	SD (%)
Tuned to fishing mortality								
F increasing	2.9	3.0	−27.3	20.4	−2.1	3.4	23.6	27.7
F decreasing	23.1	14.0	−24.1	24.2	8.4	3.5	40.9	27.7
F constant	15.8	8.9	−21.5	24.3	4.7	2.3	38.5	29.9
Tuned to proportion-at-age								
F increasing	3.5	1.6	−10.8	14.8	−2.5	1.6	−3.8	14.0
F decreasing	26.8	13.3	−4.4	22.8	10.2	4.5	−1.3	13.6
F constant	17.7	7.9	1.6	19.7	5.6	2.1	−1.2	13.2

Table 3 (Continued)

D	Increasing selectivity			Decreasing selectivity		
	Mean (%)	SD (%)	Improvement in fit (%)	Mean (%)	SD (%)	Improvement in fit (%)
Tuned to fishing mortality						
F increasing	–30.0	45.3	45.7	24.3	89.8	29.5
F decreasing	–38.0	42.1	56.7	29.8	95.7	32.2
F constant	–32.8	45.2	51.9	30.7	96.0	31.6
Tuned to proportion-at-age						
F increasing	–13.5	40.0	25.6	0.5	60.0	18.5
F decreasing	–21.9	39.2	37.7	–4.6	61.7	23.8
F constant	–13.3	41.1	30.9	–2.5	59.6	21.4

[1]Bias is measured here as the relative error of the estimated value, (estimate – true) / true.
[2]The Stock Synthesis program estimates average biomass for each year of the input data series. The values here are the averages and standard deviations of the ten annual estimates.
[3]The Stock Synthesis program can estimate recruitment for each year of the input data series. The values here are the averages and standard deviations of the ten annual estimates.
[4]The "improvement in fit" is measured here by the relative increase in the value of the log-likelihood when the Stock Synthesis program estimates the annual recruitment rather than being given the true values. This is defined as

$$(L' - L) / L$$

where L is the value of the log-likelihood when the program was given the true annual recruitment values, and L' is the value of the log-likelihood when the program estimated the annual recruitment values. The log-likelihood is given by

$$\sum_y J_y \cdot \sum_a p_{y,a} \log_e(p_{y,a});$$

where J_y is the number of fish in the (y)th catch-at-age sample, $p_{y,a}$ is the observed proportion of fish in the (y)th sample that are from the (a)th age class, and $\hat{p}_{y,a}$ is the predicted proportion of fish in the (y)th sample from the (a)th age class (Methot, 1990).

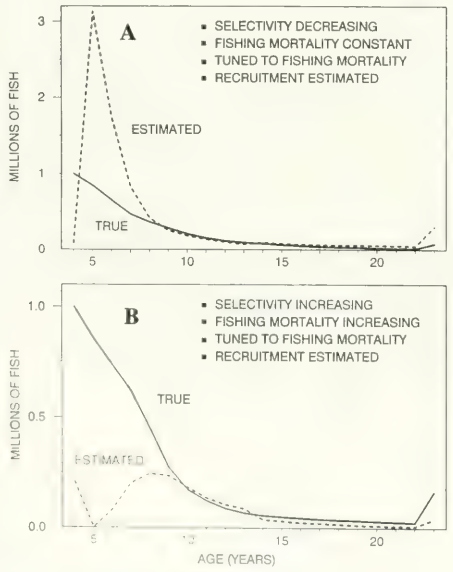

Figure 3

True versus estimated age distributions. For the age distribution shown in the upper panel (**A**) the Stock Synthesis program produced an estimate of average biomass in the final year that was 74% too large. For the distribution in the lower panel (**B**) the program produced an estimate that was 59% too small.

Sensitivity of other stock assessment programs that assume constant selectivity

The results of the experiments with CAGEAN and the multiplicative catch-at-age model indicate that these assessment methods, like the Stock Synthesis program, are also sensitive to violations of the constant selectivity assumption. When selectivity increased, both the Stock Synthesis and CAGEAN programs incorrectly produced a large decrease in the biomass of the simulated population during the last few years, and large declines in recruitment (Fig. 5). The multiplicative catch-at-age model does not provide estimates of biomass, but its estimates of relative recruitment were almost identical to those from the CAGEAN program. When selectivity decreased, the Stock Synthesis program and the CAGEAN program both overestimated the biomass in the last few years, but the estimates from the CAGEAN program were grossly incorrect (Fig. 6). Both the CAGEAN program and the multiplicative catch-at-age model estimated very large increases in recruitment.

Sensitivity of the Stock Synthesis program when applied to data from a heavily exploited stock

When the Stock Synthesis program was applied to data for a simulated population suffering heavy exploitation, the program produced estimates of biomass and recruitment that were even more biased than in the

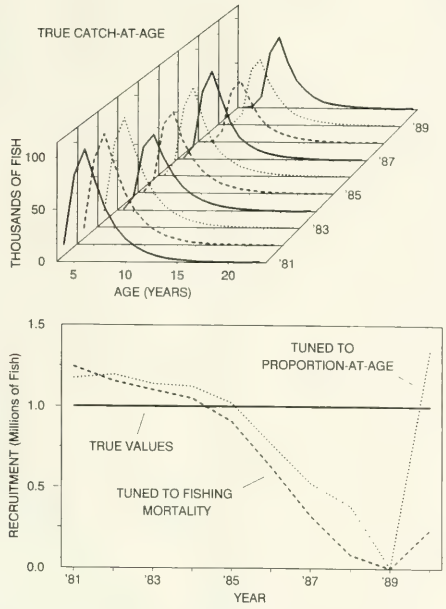

Figure 4

Trends in selectivity induce trends in recruitment. True catches-at-age (upper panel) shift through time towards older fish because of the changes in selectivity. Fishing mortality was constant for the entire period. The Stock Synthesis program attempted to mimic the changes in catch-at-age by generating estimates of recruitment that had a decreasing trend (lower panel).

earlier experiments with the simulated stock of widow rockfish. With increasing selectivity, the bias in the estimated average biomass in the final year was –86% (Fig. 7) as opposed to the bias of –54% found earlier (Table 3A; selectivity increasing, tuned to fishing mortality, fishing mortality constant, and recruitment estimated). With decreasing selectivity, the estimated average biomass in the final year was 213% too high (Fig. 8); in the earlier experiment the corresponding estimate was only 74% too high (Table 3A; selectivity decreasing, tuned to fishing mortality, fishing mortality constant, and recruitment estimated).

Discussion

In the experiments described in this paper, the assessment programs were unable to fit exactly the simulated catch-at-age data because the catch model was mis-specified. Selectivity was falsely assumed constant,

Table 4

Sensitivity analysis of the Stock Synthesis program. Bias in the estimated average biomass in the final year when selectivity varied randomly.

	Known recruitment		Estimated recruitment	
	Mean (%)	SD (%)	Mean (%)	SD (%)
Tuned to fishing mortality				
F increasing	–1.4	0.8	–19.7	21.9
F decreasing	11.3	4.4	–17.0	24.0
F constant	7.8	3.5	–18.6	23.2
Tuned to proportion-at-age				
F increasing	–0.1	0.8	–4.2	3.5
F decreasing	13.3	4.6	–8.5	5.7
F constant	8.9	3.8	–6.0	4.9

and the biomass and abundance estimates were biased as a consequence. In any real application, not only would the assessment program be ignorant of the true model structure, but the program would also have to contend with "noise" in the data due to measure-

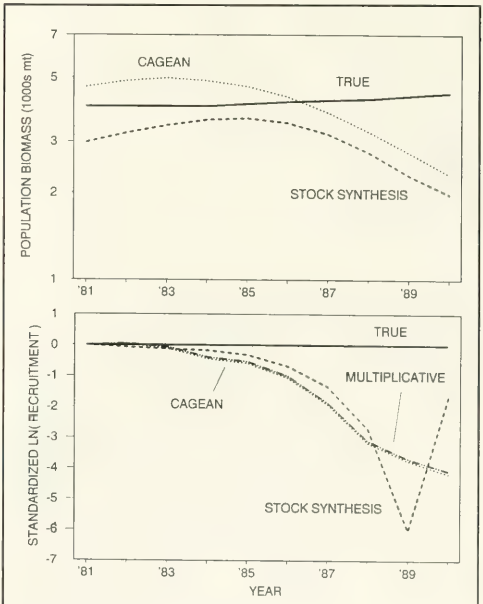

Figure 5

Estimated biomass and recruitment from different assessment programs with selectivity increasing. Three assessment programs, all of which assume constant selectivity, were applied to the simulated widow rockfish data in which selectivity shifted to older ages and fishing mortality was constant (Table 2A). All three programs were sensitive to the shifts in selectivity.

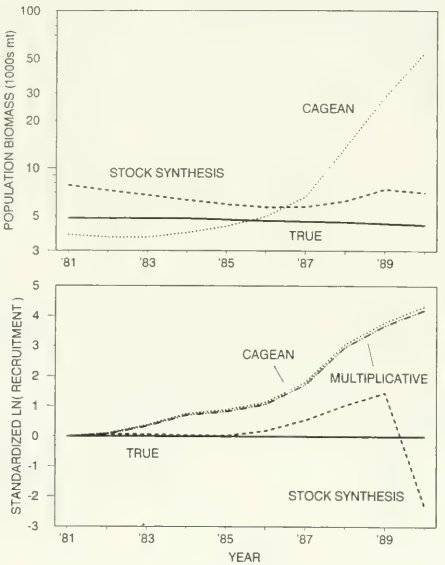

Figure 6

Estimated biomass and recruitment from different assessment programs with selectivity decreasing. The three assessment programs were also applied to the simulated widow rockfish data in which selectivity shifted to younger ages and fishing mortality was constant (Table 2B). Again, all three programs were sensitive to the shifts in selectivity.

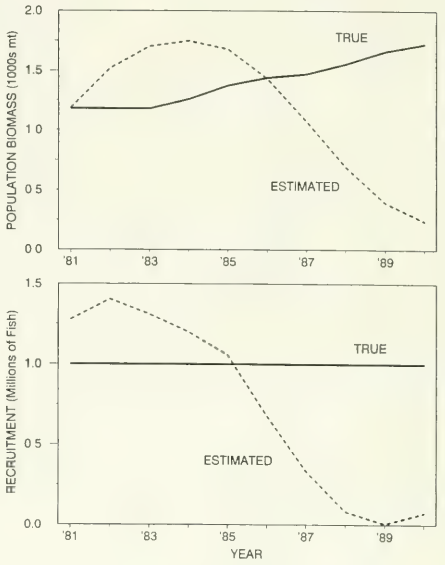

Figure 7

Stock synthesis estimates of biomass and recruitment for a heavily fished stock with selectivity increasing. The Stock Synthesis program was applied to simulated widow rockfish data in which the fishing mortality rate was constant at 0.60 per year, the natural mortality rate was 0.30 per year, and selectivity shifted to older ages. The estimates were even more biased than the ones from the corresponding earlier experiment.

ment errors and to randomness in the catch process. A complete analysis of the problem would measure how the assessment program transforms variability in the catch-at-age data into variability in the resulting estimates (e.g., Kimura, 1989).

Because the catch model with constant selectivity has fewer unknown parameters, when applied to noisy catch-at-age data, the assessment program's estimates could obtain greater precision (but not accuracy) by assuming constant selectivity, even though the assumption was incorrect[3]. However, it seems unlikely that noise in the data could ever reduce the bias resulting from a structural deficiency in the underlying catch-at-age model.

In the experiments with the simulated catch-at-age data, the year-to-year changes in selectivity were not particularly drastic, but I know of no studies to support my conjecture that they are realistic for the stock of widow rockfish. The simulated changes in selectivity were comparable to those observed by Houghton and Flatman (1981) for North Sea cod and by Gordoa and Hightower (1991) for Cape hake. The fact that experiments with "random" changes in selectivity produced results similar to those from experiments with trends in selectivity confirm that the biased estimates were not just artifacts of having a simple trend in selectivity, rather than a more complex type of variation.

One surprising result of the experiments with different assessment methods was the large discrepancy between the estimates from Stock Synthesis and CAGEAN when selectivity decreased (Fig. 6). The two programs differ primarily in how they account for vari-

[3]John Shepherd, Ministry of Agriculture, Fisheries, and Food, Fisheries Laboratory, Lowestoft, Suffolk, NR33 0HT, U.K., pers. commun. April 1992.

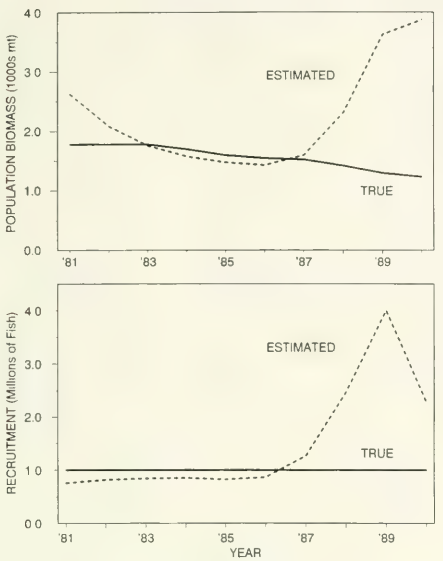

Figure 8

Stock synthesis's estimates of biomass and recruitment for a heavily fished stock with selectivity decreasing. The Stock Synthesis program was applied to simulated widow rockfish data in which the fishing mortality rate was constant at 0.60 per year, the natural mortality rate was 0.30 per year, and selectivity shifted to younger ages. Again, the estimates were more biased than the ones from the corresponding earlier experiment.

ability in catch-at-age. Stock Synthesis assumes multinomial error, but CAGEAN assumes lognormal error. Using simulation techniques, Kimura (1990) directly compared estimates derived by using these alternative assumptions and found little difference between the estimates obtained.

Another difference between Stock Synthesis and CAGEAN is in their method for modeling selectivity. The Stock Synthesis program uses a double-logistic curve to model selectivity as a smooth function of age, but the CAGEAN-PC program estimates the selectivity coefficients independently for each age. Because the true selectivity coefficients were based on double-logistic curves, this difference between the two programs should be only a minor factor. Kimura (1990) found that the assumption of a functional form for selectivity had little effect on his analyses of simulated catch-at-age data, provided the true selectivity coefficients conformed to the general shape of the selectivity function.

The dilemma for the assessment scientist is to develop a framework for analyzing fisheries data that is simple to use and yet is adequate to describe the complex dynamics of a living and constantly changing fish stock. The assessment scientist has the difficult task of interpreting diverse and possibly conflicting information. He needs tools with which to weigh these data objectively and to draw from them reliable conclusions about the status of a stock. Stock Synthesis, CAGEAN, and the multiplicative catch-at-age analysis were designed to be such tools.

In principle, one can use the Stock Synthesis and CAGEAN programs to test for shifts in selectivity. Both programs support a limited form of variable selectivity in which abrupt changes can occur at pre-specified times with constant selectivity during the intervening periods. With either program it is a relatively simple, but tedious, matter to re-analyze the data by using different times for the selectivity changes. For example, I applied the CAGEAN program to the simulated widow rockfish data set given in Table 2A, with the data partitioned into two periods of constant selectivity, and I allowed the timing of the selectivity change to occur between all possible adjacent years. The resulting pattern in the residual sums of squares[4] (Fig. 9, upper panel) clearly indicates the true change in selectivity that occurred between the third and fourth years. I repeated the process with the data series partitioned into three periods of constant selectivity, one for the first three years, and the other periods for the remaining years. The CAGEAN program was able to fit the data exactly when selectivity changed between the seventh and eighth years (Fig. 9, lower panel).

Although the current versions of the Stock Synthesis and CAGEAN programs can be applied in the above fashion to explore systematically for changes in selection, such a brute force approach to model building is extremely repetitious and time-consuming. I hope that the next generation of stock assessment programs will automate this process in a manner similar to existing stepwise regression programs, and thereby allow the user to test rigorously for variations in selectivity.

The model used for stock assessment should not force the data to fit a particular structure unless there is evidence that the structure is real or that it does not appreciably distort the results of the assessment. The

[4]CAGEAN defines the residual sum of squares as

$$\sum [\log_e(c) - \log_e(\hat{c})]$$

where c and $\hat{c}$ are the observed and predicted catch-at-age.

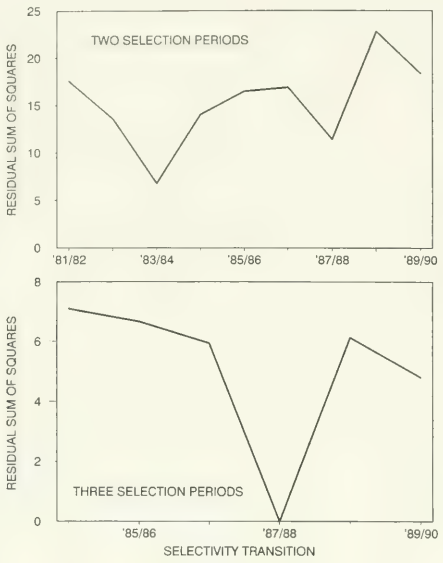

Figure 9

Residual sum of squares resulting from applications of CAGEAN with changes in selectivity. The CAGEAN program was applied to the simulated widow rockfish data in which selectivity shifted to older ages and fishing mortality was constant (Table 2A). In the upper panel the selectivity coefficients were allowed to vary abruptly between adjacent years, thereby dividing the data into two periods of constant selectivity. The minimum in the residual sum of squares corresponds to the true change in selectivity that occurred between 1983 and 1984. In the lower panel, selectivity was constant for the first three years but was allowed to vary between adjacent years in the remaining period. The zero in the residual sum of squares corresponds to the true change in selectivity that occurred between 1983 and 1984. In these analyses the age at 100% selection was fixed at age 7 for the first selectivity period, at age 8 for the second period, and at age 9 for the third.

situation is analogous to an application of two-way analysis of variance (ANOVA). In fitting a two-way ANOVA model, one should test for a significant interaction term before drawing inferences about the main effects. By the same logic, in fitting a catch-at-age model, one should test for changes in selectivity before concluding that stock size has been increasing or decreasing.

I have no real evidence of changes from year to year in the selectivity for widow rockfish off the coasts of Washington, Oregon, and California. However, the work described in this paper demonstrates that an incorrect assumption of constant selectivity can seriously distort an assessment of widow rockfish stock size. Furthermore, there is at least one reason to suspect that selectivity for widow rockfish has varied through time. During the early years of the directed fishery for widow rockfish, vessels targeted schools of fish using midwater trawls. With the rapid expansion of the fishery, the Pacific Fishery Management Council began imposing increasingly restrictive limits on the amounts of widow rockfish that could legally be landed from any single fishing trip (Gunderson, 1984). One result of these "trip limits" was a reduction in the landings by midwater trawlers relative to the landings by bottom trawlers. Midwater trawlers accounted for roughly 75% of the widow rockfish landings in Oregon during 1984 through 1988, but they accounted for only 60% in 1990, and for less than 50% in 1991. It seems quite probable that the midwater trawls have different selection characteristics than do bottom trawls, and that the shift from a midwater fishery to a bottom fishery would cause changes in selectivity.

Any stock assessment model will have to make simplifying assumptions to summarize succinctly the major features of the data. However, in my view the assumption of constant selectivity is an unnecessary and misleading oversimplification, use of which can result in catch quotas that are either needlessly conservative, resulting in immediate losses to the fishing industry, or that are excessively liberal, producing losses in recruitment and catches at a more distant time.

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Genetic analysis of the population structure of yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean*

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Abstract.—The genetic basis of the population structure of yellowfin tuna, *Thunnus albacares*, in the Pacific Ocean was investigated with restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). Samples of 20 yellowfin tuna were examined from each of five Pacific locations and one Atlantic location. MtDNA analysis with 12 informative restriction endonucleases demonstrated considerable genetic variation, as evidenced by an overall nucleon diversity of 0.84 and a mean nucleotide sequence diversity of 0.91%. Estimates of within-sample variation were remarkably consistent across all six locations. Despite high levels of variation, there was no evidence of genetic differentiation among samples. Common genotypes occurred with similar frequencies in all samples, and, with one exception, all genotypes that were represented by more than one individual occurred at more than one location. We could not reject the null hypothesis that all yellowfin tuna share a common gene pool. Our results are consistent with the alternate hypothesis that there is sufficient gene flow within the Pacific, as well as between the Atlantic and Pacific oceans, to prevent the accumulation of significant genetic differentiation.

Yellowfin tuna (*Thunnus albacares*) occur in the tropical and subtropical oceans and support major commercial fisheries throughout their range (Collette and Nauen, 1983). The economic importance of this species is indicated by high annual catches that have increased from 596,764 metric tons (t) in 1981 to 986,529 t in 1990, of which 66 to 69% were from the Pacific Ocean (FAO, 1992). Recently, purse-seine and longline fisheries in the western Pacific (120°E to about 180°) provided a major share of yellowfin tuna landings, with a catch of 342,921 t in 1990 (Lawson, 1991). In the eastern Pacific (east of 130°W) record landings near 270,000 t occurred in each of the past 3 years[1].

A thorough understanding of yellowfin tuna population structure is necessary for the effective management of this economically important, marine resource. A variety of studies, including tagging, morphometric, fishery statistic and genetic analyses, have been used to infer population structure. However, the proposed population structures differed.

Tagging studies have indicated that movements of yellowfin tuna in the Pacific Ocean tend to be geographically restricted. Fink and Bayliff (1970) analyzed tag return data in the eastern Pacific and proposed a northern and southern group of fish with some exchange between groups. There was very limited westward movement of tagged fish reported in the study; however, as the eastern Pacific fishery expanded westward in subsequent years, several returns were obtained from farther offshore indicating possible mixing between eastern and central Pacific fish (Bayliff, 1984). In the western Pacific tagging studies showed that most individuals remained within the western Pacific region and did not make extensive movements (Itano and Williams, 1992; Lewis, 1992). Although the majority of recaptured yellowfin tuna in all studies showed limited movement, some returns were obtained which demonstrated the potential for fish to move large dis-

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[1]Anonymous. 1992. Inter-American Tropical Tuna commission, Annual Report, 1991.

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tances and between regions (Fink and Bayliff, 1970; Bayliff, 1984; Itano and Williams, 1992).

Population structure was indicated by investigations of both meristic and morphometric characters which revealed significant differentiation among yellowfin tuna from the eastern, central, and western Pacific regions (Schaefer, 1955; Kurogane and Hiyama, 1957), as well as clinal character variation across the equatorial Pacific (Royce, 1964). Further investigation using discriminant function analysis of morphometric variables suggested mixing occurs between morphologically differentiated northern and southern yellowfin tuna of the eastern Pacific (Schaefer, 1989), as well as across the Pacific (Schaefer, 1991, 1992).

Analysis of fishery data also suggests population structuring of yellowfin tuna within the Pacific. Kamimura and Honma (1963) provided evidence for two or more semi-independent subpopulations based on size composition and catch data of equatorial Pacific yellowfin tuna from longline landings. Suzuki et al. (1978) examined longline and purse-seine length composition data and suggested the existence of semi-independent eastern, central, and western Pacific subpopulations. Additionally, homogeneity within the western Pacific was indicated by the widespread distribution of fish contaminated by radioactivity resulting from the 1954 U.S. nuclear tests at Bikini Atoll (Suzuki et al., 1978).

While the results of several analyses suggest yellowfin tuna exhibit population structure within the Pacific Ocean, genetic analyses have revealed no significant genetic differentiation. Suzuki (1962) reported that the blood agglutinogen Tg2 occurs in similar frequencies in samples from the Indian Ocean and the eastern Pacific. Additionally, allozyme analysis did not reveal genetic differentiation between samples of yellowfin tuna collected off Hawaii (n=529) and Baja California (n=207) at the polymorphic serum esterase locus, although overall variation was low (Fujino, 1970). Preliminary evidence for frequency differences occurring at two other loci (phosphoglucose isomerase and transferrin A) was reported for both within and between samples of Atlantic and Pacific yellowfin tuna[2,3]. However these loci have not been used to examine population structure.

Our understanding of the population structure of yellowfin tuna in the Pacific Ocean remains problematic. Much evidence is available which suggests that population structure exists, yet genetic analyses did not reveal differentiation among samples collected from distant locations. To further examine the genetic basis of the population structure of Pacific yellowfin tuna we employed restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). Because mtDNA evolves rapidly (Moritz et al., 1987; Brown et al., 1979) and displays considerable polymorphism within animal populations (Avise and Lansman, 1983), mtDNA analyses have been useful in revealing population structure within marine fishes (Ovenden, 1990). Using this technique, we demonstrated considerable genetic variability within yellowfin tuna, but we could not reject the null hypothesis that samples share a common gene pool.

Materials and methods

Hearts were taken from 50 yellowfin tuna at each of five Pacific locations and one Atlantic location (Fig. 1); however, only 20 specimens per location were analyzed. Samples from the Pacific were collected during 1990 at Manta, Ecuador (ECU); Revillagigedo Islands, Mexico (MEX); Oahu, Hawaii (HAW); Manus Island, Papua New Guinea (PNG); and New South Wales, Australia (AUS). The sample from the Atlantic was collected during 1991 at Hatteras, North Carolina (ATL). Hearts were dissected within 12 hours of capture and placed on crushed ice. Hearts from fish collected in the Pacific were frozen at –20°C and shipped to the Inter-American Tropical Tuna Commission, La Jolla, CA, where they were stored at –20°C for more than one year before shipment to our laboratory. Hearts from fish collected in the Atlantic were transported on wet ice and frozen at –70°C within four hours of dissection.

MtDNA was purified from 3 g of heart tissue from Atlantic specimens following the CsCl-ethidium bromide gradient centrifugation protocol of Lansman et al. (1981). MtDNA yields averaged about 350 ng of supercoiled mtDNA per g of heart tissue. Aliquots of mtDNA were digested with the following 12 informative restriction endonucleases (Stratagene and BRL) according to the manufacturers' instructions: *Apa*I, *Ava*I, *Ban*I, *Bcl*I, *Bgl*I, *Dra*I, *Eco*RI, *Hin*dIII, *Nci*I, *Pst*I, *Pvu*II and *Xho*I. Restriction fragments were end-labeled with a mixture of all four α-^{35}S-dNTP's by using the Klenow fragment, electrophoresed at 2 volts/cm overnight in 1% agarose gels, and visualized by autoradiography (Sambrook et al., 1989).

Yields of supercoiled mtDNA from Pacific specimens were low, possibly due to sub-optimal storage conditions. For these specimens, mtDNA-enriched genomic DNA was isolated from 4 to 6 g of heart tissue following the protocols of Chapman and Powers (1984), modified by the omission of sucrose step gradients and the

[2] Anonymous. 1977. Inter-American Tropical Tuna Commission, Annual Report, 1976.

[3] Anonymous. 1978. Inter-American Tropical Tuna Commission, Annual Report, 1977.

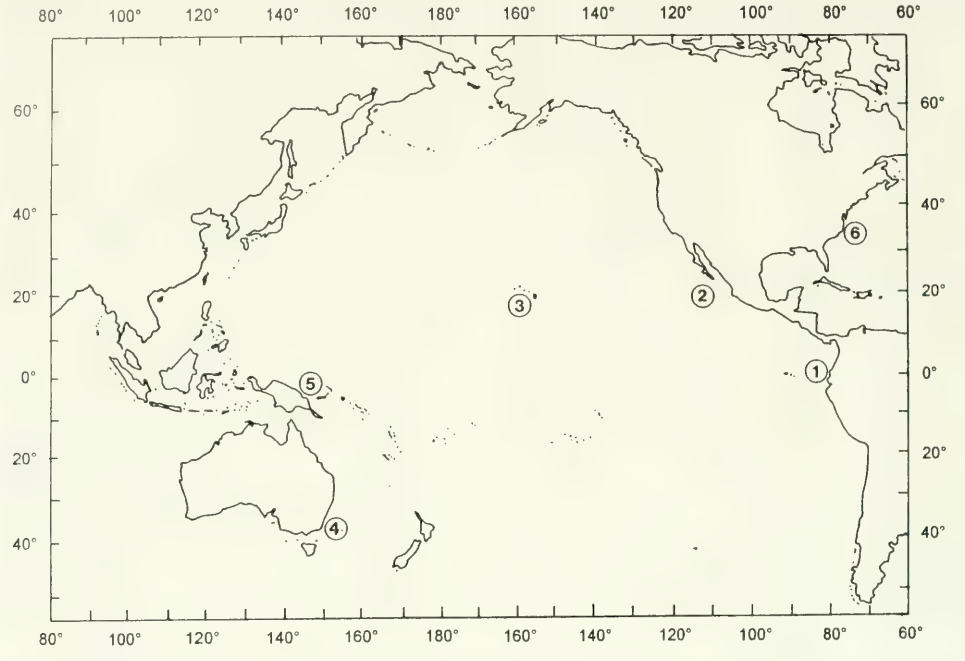

Figure 1

Thunnus albacares. Location of sampling sites used in this analysis: (1) Manta, Ecuador (ECU); (2) the Revillagigedo Islands, Mexico (MEX); (3) Oahu, Hawaii (HAW); (4) New South Wales, Australia (AUS); (5) Manus Island, Papua New Guinea (PNG); and (6) Hatteras, North Carolina (ATL).

use of 1.5% sodium dodecyl sulfate for mitochondrial lysis. Following restriction enzyme digestion and horizontal agarose gel electrophoresis, DNA fragments were transferred to nylon membranes by Southern transfer (Sambrook et al., 1989) and immobilized by long-wave UV irradiation. Prehybridization was conducted for two hours at 42°C in 50% formamide, 5× SSC, 5× Dendhardt's solution, 0.025 mM $NaPO_4$, pH 6.5, and 100 µg/mL heat denatured calf thymus DNA. Probe DNA (mtDNA purified from extra specimens from the Atlantic) was nick-translated to incorporate biotin-7-dATP (BRL), and separated from unincorporated nucleotides by size exclusion chromatography. One µg of probe was added to the prehybridization solution for each 200 cm^2 blot and allowed to hybridize overnight at 42°C. Following post-hybridization washes (Sambrook et al., 1989), mtDNA fragments were visualized with the BRL BluGene Non-Radioactive Nucleic Acid Detection Kit.

A 12-letter composite mtDNA genotype, indicating the fragment pattern for each restriction enzyme, was developed for each individual. Estimates of nucleon diversity (h) for each sample and for the pooled samples were computed following Nei (1987). Nucleotide sequence divergences among genotypes were estimated by using the site method of Nei and Li (1979). Estimates of nucleotide sequence diversity (p) within each sample, and mean nucleotide sequence divergences among samples (corrected for within-sample diversities) were computed following Nei (1987). Nucleotide sequence divergences were clustered by the unweighted pair-group method with arithmetic means (UPGMA) by using the average linkage algorithm of the SPSS-X statistical package (Norusis, 1988). Values of G_{st}, a measure of heterogeneity between samples, were estimated from sample genotype frequencies (Nei, 1987), and values of N_fm, the absolute number of migrants between samples, were determined from the relation

$N_em = (1/G_{st} - 1)/2$ (Birky et al., 1983; Nei, 1987). Chi-square analysis was conducted by using the Monte-Carlo method of Roff and Bentzen (1989) with 1000 randomizations of the data to evaluate heterogeneity of genotype frequencies among samples without combining rare genotypes.

Results

Analysis of mtDNA from 120 yellowfin tuna with 12 restriction enzymes revealed a total of 34 genotypes, comprising 83 unique fragments. The most common genotype consisted of 52 fragments, representing a survey of 304 bp, or about 1.8% of the mtDNA genome. The mean size of the yellowfin tuna mtDNA genome, determined from the most common restriction fragment profiles for each of the 12 restriction enzymes, was 16,549 ± 309 bp (SD).

RFLP analysis of yellowfin tuna mtDNA demonstrated considerable variation. While four restriction enzymes, *Ava*I, *Dra*I, *Hin*dIII, and *Xho*I, showed no variation, the remaining eight revealed two to seven restriction morphs each. Of the 34 genotypes, two were represented by 20 or more individuals, five were represented by four or more individuals, and 20 genotypes occurred only once (Table 1). Within-sample nucleon diversities were high and showed little variation among samples, ranging from 0.82 to 0.86, with a value of 0.84 for the pooled samples (Table 2). Mean nucleotide sequence diversities were also high, ranging

Table 1

Distributions of mtDNA genotypes among samples of yellowfin tuna, *Thunnus albacares*. Letters represent fragment patterns produced by the following enzymes (left to right): *Eco*RI, *Hin*dIII, *Pst*I, *Dra*I, *Ava*I, *Puv*II, *Nci*I, *Ban*I, *Bcl*I, *Bgl*I, *Xho*I, and *Apa*I. A description of fragment sizes is available upon request.

	mtDNA genotype	Sampling location						
		ECU	MEX	HAW	AUS	PNG	ATL	Total
1	AAAAAAAAAAAA	7	6	7	8	8	7	43
2	BAAAAAAAAAAA	2	5	3	4	3	3	20
3	BAAAAABAAAAA	3	—	1	—	1	1	6
4	AAAAAAAAECAA	1	1	—	2	—	2	6
5	AAAAAAAABAAA	—	—	—	1	1	2	4
6	AAAAAABAEAAA	1	—	1	—	—	1	3
7	AAAAAABABAAA	2	1	—	—	—	—	3
8	AABAAAAAAAAA	—	2	—	1	—	—	3
9	AAAAAAABAAAA	—	—	1	—	1	—	2
10	AAAAAAAABBAA	—	—	1	1	—	—	2
11	BAAAAAAAAAAB	—	—	1	—	—	1	2
12	BAAAAAAACAAA	—	—	1	—	1	—	2
13	AAAAAAAAEAAF	—	1	—	—	1	—	2
14	AAAAAABAAAAA	—	—	2	—	—	—	2
15	AAAAAAAAAAAB	—	—	—	1	—	—	1
16	AAAAABAAAAAA	—	—	—	—	—	1	1
17	AAAAAAAAAAAC	—	—	—	—	1	—	1
18	AAAAAAAAAAAD	—	—	—	—	1	—	1
19	AAAAAAAAFAAA	—	—	—	—	1	—	1
20	AAAAAAAAAAAF	—	—	1	—	—	—	1
21	AABAAAAABAAA	—	—	—	—	—	1	1
22	BABAAAAAAAAA	—	—	1	—	—	—	1
23	AAAAAABAAAAE	—	—	—	1	—	—	1
24	AAAAAAAADAAB	—	—	—	—	1	—	1
25	CAAAAABAAAAA	1	—	—	—	—	—	1
26	AABAAAAAAAAG	1	—	—	—	—	—	1
27	AABAAAAAEAAA	1	—	—	—	—	—	1
28	AAAAAABAAAAB	—	1	—	—	—	—	1
29	BAAAAAAAAAAD	—	1	—	—	—	—	1
30	BAAAAAAABBAA	—	1	—	—	—	—	1
31	BAAAAABABAAA	—	1	—	—	—	—	1
32	BAAAAABAGAAA	1	—	—	—	—	—	1
33	AAAAAABAADAA	—	—	—	—	—	1	1
34	AAAAAAACFEAA	—	—	—	1	—	—	1
Total		20	20	20	20	20	20	120

Table 2

Genetic variation within samples of yellowfin tuna, *Thunnus albacares*, expressed as nucleon diversity (h) and percent nucleotide sequence diversity (p).

Sampling location	Nucleon diversity (h)	Nucleotide sequence diversity (p) %
ECU	0.863	1.04
MEX	0.863	0.955
HAW	0.868	0.799
AUS	0.816	0.905
PNG	0.837	0.737
ATL	0.863	0.917
Pooled	0.840	0.907

from 0.74% to 1.04%, and 1.04% for the pooled samples (Table 2).

Despite the high level of within-sample variation, there was little evidence for genetic differentiation among the six sampling sites. The two most common genotypes (1 and 2) were observed at all locations at similar frequencies (30–40%, 10–25%, respectively; Table 1). Of the 12 other genotypes that occurred in more than a single individual, 11 were found in two or more samples, and only one (genotype 14) occurred in a single sample, represented by two individuals.

Pairwise estimates of corrected nucleotide sequence divergences between samples (including the Atlantic) were low, ranging from 0.012% to 0.104%, with a mean pairwise divergence of 0.04%. Similarly, estimates of G_{st} were low, ranging from 0.011 to 0.025, and values of N_fm were correspondingly high, ranging from 19.5 to 44.5 females per generation. No clear pattern of phylogeographic structure was revealed in cluster analyses of nucleotide sequence divergences among mtDNA genotypes or sampling locations. Chi-square analysis of heterogeneity among samples was not significant, as randomizations of the data into six samples were more heterogeneous than the observed genotypic distributions 581 of 1000 times (P=0.581).

To determine an appropriate number of individuals to examine from each location and the number of restriction enzymes to employ, we compared levels of genetic variation and differentiation revealed by a pilot study of 12 individuals per location with 5 enzymes with larger analyses of up to 20 individuals per location with 12 enzymes (Table 3). Levels of variation were influenced more by increasing the number of enzymes surveyed than the number of individuals. Increasing the number of enzymes increased the number of genotypes, the nucleon diversities, and, to a lesser extent, nucleotide sequence diversities. Analysis of a greater number of individuals per location had little effect on diversity estimates with either 5 or 12 enzymes, although the ranges of within-sample diversities among locations decreased as more individuals were analyzed.

Increasing the number of individuals or the number of enzymes had little effect on levels of genetic differentiation. No significant differences were found in the distributions of genotypes among locations in Roff and Bentzen (1989) chi-square tests (Table 3). Furthermore, increasing the number of individuals in the 12 enzyme analysis did not increase the frequencies of genotypes unique to a location. Instead, many unique genotypes in the analysis of 12 individuals occurred in other locations as a greater number of individuals were used. Because increasing sample sizes from 12 to 20 individuals did not reveal greater spatial partitioning of genetic variation, we decided that 20 individuals was an appropriate sample size.

Discussion

Population structure is typically manifested as the spatial or temporal partitioning of genetic variation. Therefore, to demonstrate if population structure exists, a technique must first reveal a reasonable level of genetic variation. RFLP analysis of mtDNA revealed considerable genetic variation in yellowfin tuna. The overall nucleon diversity and mean nucleotide sequence diversity (0.84 and 0.91%, respectively) are in the up-

Table 3

Pooled percent nucleotide sequence diversities (p) and nucleon diversities (h), and respective ranges (in parentheses) among samples obtained by varying the numbers of restriction enzymes and individuals of yellowfin tuna, *Thunnus albacares*, per sampling location. Probabilities of significance result from Roff and Bentzen's (1989) chi-square analysis with 1000 randomizations of the data. The five enzymes selected for the pilot study were *Eco*RI, *Hin*dIII, *Pst*I, *Dra*I, and *Ava*I.

Design	Number of genotypes	Nucleon diversity (h)	Nucleotide sequence diversity (p) (%)	Prob.
5 enzymes 12 individuals	6	0.496 (0.41–0.64)	0.705 (0.49–0.90)	0.960
5 enzymes 20 individuals	6	0.509 (0.42–0.63)	0.714 (0.62–0.91)	0.845
12 enzymes 12 individuals	27	0.829 (0.76–0.94)	0.907 (0.66–1.22)	0.975
12 enzymes 20 individuals	34	0.840 (0.82–0.87)	0.907 (0.74–1.04)	0.581

per ranges reported for marine fishes (Avise et al., 1989; Ovenden, 1990; Gold and Richardson, 1991) including other large, pelagic fishes (Table 4).

Genetic variability in tuna species has also been demonstrated by sequence analysis of a 307-base-pair region of the mitochondrial cytochrome *b* gene of bluefin tuna, *Thunnus thynnus*; bigeye tuna, *T. obesus*; albacore, *T. alalunga*; and yellowfin tuna (Bartlett and Davidson, 1991). The sequence data presented for 33 yellowfin tuna result in a nucleon diversity of $h = 0.28$, a value that is considerably lower than the nucleon diversity of 0.84 obtained in our study. Although nucleon diversity values are greatly influenced by the number of base pairs surveyed (Nei, 1987), the number examined in this study and in Bartlett and Davidson (1991) were very close (304 and 307, respectively). This difference in nucleotide sequence diversity may reflect a slower evolutionary rate for the mitochondrial cytochrome *b* gene relative to the entire mtDNA genome.

Significant genetic differentiation among yellowfin tuna from geographically distant locations was not found. Corrected nucleotide sequence divergences averaged only 0.04%, indicating that the mean difference between two genotypes randomly chosen from any two samples was essentially the same as the difference between two genotypes randomly drawn from the same sample. The frequencies of the two most common genotypes were similar among all locations, and an overall chi-square test for heterogeneity was non-significant. Furthermore, nucleon diversities and nucleotide sequence diversities were similar among locations, although uniformity in the latter estimates was less pronounced.

Table 4

Genetic variation within selected pelagic species determined by RFLP analysis of mtDNA employing 11–13 informative enzymes. Variation is expressed as nucleon diversity (h) and percent nucleotide sequence diversity (p).

Species	Nucleon diversity (h)	Nucleotide sequence diversity (p) (%)
Thunnus albacares[1] (Yellowfin Tuna)	0.84	0.91
Thunnus alalunga[2] (Albacore Tuna)	0.60	0.31
Tetrapturus audax[3] (Striped Marlin)	0.74	0.54
Tetrapturus albidus[3] (White Marlin)	0.70	0.35
Makaira nigricans[3] (Blue Marlin)	0.86	1.99
Istiophorus platypterus[3] (Sailfish)	0.62	0.87

[1]This study.
[2]Graves and Dizon (1989) and Graves, unpublished data.
[3]Graves and McDowell, in press.

The apparent genetic homogeneity of yellowfin tuna is consistent with the hypothesis that there is genetic exchange among locations. Rare mtDNA genotypes had low frequencies of occurrence (Table 1), characteristic of high gene flow (Slatkin, 1985), a situation similar to that found in other species for which high gene flow is suggested: American eel, *Anguilla rostrata* (Avise et al., 1986); marine catfishes, Ariidae (Avise et al., 1987); weakfish, *Cynoscion regalis* (Graves et al., 1992a); and bluefish, *Pomatomus saltatrix* (Graves et al., 1992b). Low pairwise estimates of G_{st} (0.011–0.025) also indicated homogeneity in yellowfin tuna and gave rise to high N_em values (>19) which are consistent with high rates of gene flow among regions (Birky et al., 1983).

The absence of genetic differentiation between Pacific and Atlantic samples of yellowfin tuna is similar to that reported for other vagile pelagic species. RFLP analysis of mtDNA of skipjack tuna, *Katsuwonus pelamis*, and of albacore from the Atlantic and Pacific oceans revealed modest amounts of within-sample variation, but no significant differentiation was found between Atlantic and Pacific conspecifics (Graves et al., 1984; Graves and Dizon, 1989). Similarly, RFLP analysis of mtDNA of the pelagic dolphin, *Coryphaena hippurus*, revealed no significant differentiation between samples from the Atlantic and Pacific oceans[4]. However, spatial partitioning of genetic variation occurs in at least some pelagic fishes. Significant genetic differentiation was shown between Atlantic and Pacific blue marlin, *Makaira nigricans*, by direct sequence analysis of the mitochondrial cytochrome *b* gene (Finnerty and Block, 1992) and RFLP analysis of mtDNA (Graves and McDowell, in press). Similarly, differentiation was found among striped marlin samples, *Tetrapturus audax*, and sailfish, *Istiophorus platypterus*, from the Pacific Ocean by RFLP analysis of mtDNA (Graves and McDowell, in press).

There are several characteristics of yellowfin tuna which could promote gene flow among locations. Yellowfin tuna are distributed circumtropically (Collette and Nauen, 1983) and occur around the Cape of Good Hope in the southern summer (Talbot and Penrith, 1962). Tagging studies demonstrated that adults are capable of traveling large distances between Pacific regions (Fink and Bayliff, 1970; Bayliff, 1984; Itano and Williams, 1992), and are capable of undergoing trans-Atlantic crossings (Bard and Scott, 1991). The existence of suitable spawning areas throughout the

[4]Carol Reeb, University of Hawaii, pers. commun. April 1992.

tropical oceans, suggested by circumtropical occurrence of larvae (Nishikawa et al., 1985), would permit unobstructed gene flow throughout the species' distribution.

Both genetic and morphological analyses revealed considerable variation in yellowfin tuna; however, genetic analyses indicated that differentiation does not occur. Evidence that morphological characters are environmentally influenced was provided by comparison of our data to the morphological differentiation found in Schaefer (1991, 1992). In our analysis, 20 fish from four locations (Ecuador, Mexico, Hawaii, and Australia) were the same as those used in Schaefer's studies. Although no genetic differences were found among these locations, morphometric characters and gill-raker counts differed significantly, which we conclude is the result of phenotypic plasticity. The finding of greater morphological variability among Pacific samples than occurred between the Atlantic and Pacific (Schaefer and Walford, 1950) also supports the hypothesis that phenotypic plasticity is the cause of morphological differentiation in the Pacific.

The null hypothesis that yellowfin tuna in the Pacific Ocean share a common gene pool could not be rejected in this analysis. Our results were consistent with the alternate hypothesis that yellowfin tuna maintain sufficient gene flow among areas to prevent the accumulation of significant genetic differentiation. As theoretical models indicate that very low levels of migration (only a few individuals per generation) are needed to prevent genetic differentiation among large populations (Allendorf and Phelps, 1981; Hartl and Clark, 1989), the present data indicate only that some minimal amount of exchange is occurring. Other approaches are necessary to quantify the amounts of mixing among regions and to judge more accurately whether or not separate stocks should be distinguished for management purposes.

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Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboplites aurorubens* (Teleostei, Lutjanidae)*

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Abstract.–The feeding habits of the vermilion snapper, *Rhomboplites aurorubens*, were investigated to determine the role of this ecologically dominant and economically valuable species in the trophic ecology of southeastern U.S. reef habitats. Trophic ecology was studied by examining stomach contents and by comparing them to samples of benthic invertebrates and near-bottom plankton. Vermilion snapper fed on a variety of infaunal, epifaunal, and pelagic invertebrates, as well as on demersal and pelagic fishes and cephalopods. The diet was diverse but was dominated numerically by planktonic species. The benthic prey eaten were species associated with hard-bottom reef structure or were infaunal species from sand bottom areas adjacent to the reef. Many species were members of the hyperbenthos or demersal zooplankton and were apparently consumed in the water column during their nocturnal emergence from the sand or reef. Small crustaceans, especially copepods, sergestid decapods, and larvae of barnacles, stomatopods and decapods, dominated the diet of small (<50 mm SL) vermilion snapper. Larger decapods, fishes, and cephalopods were more important in the diet of larger vermilion snapper. Vermilion snapper, although reef associated, does not feed heavily on reef species, and may be important in transferring energy from the water column and adjacent sandy areas to the reef.

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The vermilion snapper, *Rhomboplites aurorubens*, is the most abundant lutjanid in the recreational and commercial fisheries of the southeastern U.S. (Grimes et al., 1982), and is a dominant component of the reef-associated ichthyofauna off the Carolinas and Georgia (Sedberry and Van Dolah, 1984). Because of its abundance and habit of foraging on small pelagic crustaceans (Grimes, 1979), vermilion snapper may be an important trophic link between the water column and those reef habitats where it schools during resting periods. If vermilion snapper also forages on infaunal benthos in adjacent sandy areas, it may be very important in the trophic coupling between the reef and surrounding expansive sandy areas. Vermilion snapper is also fed on by other predatory fishes (Sedberry, 1988) and thus may provide trophic links among top-level carnivores and the infauna, holozooplankton, demersal zooplankton (*sensu* Alldredge and King, 1977), and reef benthos.

Predation by fishes has been shown to be important in transferring energy from the water column or adjacent sand bottom areas to reef habitats (Bray et al., 1981; Meyer and Schultz, 1985; Rothans and Miller, 1991). Although information on feeding is available for some species of reef-associated fishes off the southeastern United States (Manooch, 1977; Grimes, 1979; Sedberry, 1985, 1987, 1988), the importance of reef bottom versus adjacent water column and sand bottom habitats as feeding grounds is poorly understood. These reefs support not only a variety of large sessile invertebrates (e.g., sponges, corals, tunicates) and associated motile organisms (Struhsaker, 1969; Wenner et al., 1983) but also a greater faunal abundance, diversity, and biomass than adjacent sand bottom areas of the open shelf (Struhsaker, 1969; Wenner, 1983; Wenner et al., 1983). Because of the rocky outcrops and the warming influence of the Florida Current, these reefs support tropical and subtropical families of fishes, and many economically valuable serranids, haemulids, sparids, and lutjanids, including vermilion snapper (Miller and Richards, 1980; Chester et al., 1984). The greater biomass and diversity of rocky reef habitats, compared with

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sandy areas, may be the result of trophic links through reef-asssociated fishes, such as vermilion snapper, with other ecotopes on the shelf.

While an important component of regional reef ecosystems and fisheries, vermilion snapper and demersal-feeding fishes, such as red porgy (*Pagrus pagrus*) are being overfished (Low et al., 1985; Collins and Sedberry, 1991). As a result of this increased fishing pressure, vermilion snapper has increased in abundance relative to *P. pagrus* and other overexploited reef fishes off the southeastern United States, and the importance of its functional role in reef ecosystems may have changed. Increased fishing pressure since the late 1970's has also apparently caused a concomitant decrease in mean length and a decrease in size at maturity of vermilion snapper (Collins and Pinckney, 1988; Collins and Sedberry, 1991). If small vermilion snapper consume different prey than do large vermilion snapper and if average fish size is decreasing in the region, the trophic structure of reefs may be affected.

The objectives of this study were to describe the feeding habits of vermilion snapper and to evaluate its relative dependence on hard-bottom benthos, sand-bottom infauna, demersal zooplankton (Alldredge and King, 1977, 1985; Porter and Porter, 1977), holozooplankton (Cahoon and Tronzo, 1992) and nekton as food. An additional purpose was to describe differences in feeding habits with size.

Methods

Stomachs from vermilion snapper were collected during six cruises in 1980 and 1981 from 11 reef stations off South Carolina and Georgia. Stations were located in each of three depth zones representing the inner shelf (16–22 m depth, three stations), middle shelf (23–37 m depth, four stations) and outer shelf (46–69 m depth, four stations). Delineation of depth zones was based on distribution of fish assemblages as noted in previous studies and on community analysis of catches in the present study (Struhsaker, 1969; Miller and Richards, 1980; Sedberry and Van Dolah, 1984). Fishes were collected primarily with a roller-rigged 40/54 high rise trawl (Hillier, 1974); a few were captured with traps or hook-and-line. Sampling was conducted during the day and at night on hard-bottom reef habitat that was mapped for each station by means of underwater television. Detailed descriptions of station locations and fish sampling techniques have been described elsewhere (Sedberry and Van Dolah, 1984; Wenner et al., 1984).

Standard lengths (SL in mm) were measured at sea. Stomachs were removed, individually labeled, and fixed in 10% seawater-formalin. Because of limited space and very large catches, only those stomachs that appeared to contain ingesta were preserved. No attempt was made in the field to determine the percentage of stomachs with food. Small (<50 mm SL) vermilion snapper were preserved whole and dissected in the laboratory. Fixed stomachs and small individuals were washed in tap water and transferred to 50% isopropyl alcohol.

Contents of individual stomachs were sorted by taxa and counted. Volume displacement of food items was measured in a graduated cylinder or estimated by using a 1×1 mm grid (Windell, 1971). The relative contribution of food items to the diet was determined by using three methods:

$$\text{percent frequency occurrence, } F = \frac{\text{number of stomachs with prey taxon}}{\text{number of stomachs with food}} \cdot 100$$

$$\text{percent numerical abundance, } N = \frac{\text{number of individuals of prey taxon}}{\text{total number of prey items}} \times 100$$

$$\text{percent volume displacement, } V = \frac{\text{volume displacement of prey taxon}}{\text{total volume of all prey items}} \cdot 100 .$$

These values are presented only for those prey species that occurred with a frequency of at least one percent or that made up at least one percent of the total number or volume of prey. Values of F, N, and V were also calculated for higher prey taxa, for stomachs pooled by 50-mm intervals of SL of vermilion snapper. The chi-square statistic (Tyler, 1979) was used to test for significance (0.05 level) of feeding heterogeneity between predator size classes.

To determine selection of prey type and predator feeding habitat, stomach samples were compared to samples from the potential prey environment by using Ivlev's index of electivity (Ivlev, 1961), calculated as

$$E = \frac{r_i - p_i}{r_i + p_i} ,$$

where: E = electivity for the ith potential prey species; r_i = percent by number of species i in the diet; and p_i = percent by number of species i in samples from the environment. Electivity values range from –1 to +1. Negative values imply that the species is avoided, not preferred, only incidentally ingested, or unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species that occur in a different habitat than that sampled by the prey sampler. A value near zero im-

plies no selectivity by the predator, that is to say the fish is feeding on the prey in proportion to the prey's relative abundance in samples taken in the habitat.

The electivity index was calculated for species that were numerically dominant in prey environment samples or in fish stomach samples. Dominant species included those that ranked among the five most abundant species within stomach or environmental samples pooled by depth zone. Prey samples and stomach collections were pooled by depth zone (inner, middle, and outer shelf) for comparison. Samples of benthic prey were obtained at the 11 reef sites during 1980 and 1981 with a diver-operated suction sampler (inner and middle shelf) or a grab sampler (outer shelf). Details of benthic sampling are provided elsewhere (Wenner et al., 1983; Wenner et al., 1984) and are only summarized here. Briefly, divers obtained five replicate suction samples during the day at each inner and middle shelf reef site by scraping the hard reef substrate enclosed by a 0.1-m^2 quadrat box while simultaneously sucking with an airlift device similar to that described by Chess (1979). Suction samples were collected in 1.0-mm mesh bags.

At the outer shelf stations, where water depth precluded the use of the suction device operated by divers, quantitative 0.1 m^2-samples were collected in reef habitat with a modified Smith-McIntyre grab. After retrieval, each sample was sieved through a 1.0-mm sieve and retained organisms were identified and counted. Most (75.0%) grab samples were taken during the day.

Additional sampling was conducted to compare stomach contents with potential prey species occurring in the near-bottom water column above the reef. To determine extent of feeding on the near-bottom plankton, electivity values were calculated for samples obtained with an epibenthic plankton sled and compared with those from the suction and grab samples. The sled was similar to that described by Brattegard and Fosså (1991) but had a mouth opening of 0.5 m^2 and runners that permitted it to sample 0.5 m off the bottom. The sled also had a mouth-opening mechanism designed to fish only when it was in contact with the bottom. A 0.947-mm mesh net was attached to the sled and two ten-minute tows were made per station at night to minimize net avoidance. Sled collections for invertebrates were made only in 1981. These samples were analyzed for decapods, stomatopods, cumaceans, and mysids, and comparisons with fish stomachs were limited to these taxa. Underwater television and diver observations were used to direct invertebrate sampling to reef habitat. Further details of all fish and invertebrate sampling can be found in Sedberry and Van Dolah (1984) and Wenner et. al. (1984).

Daytime submersible observations of vermilion snapper behavior were made during dives aimed at visually censusing (transects and point counts) reef fishes of the outer shelf on 14–15 July 1985. The submersible used was the *Sea Link I*, which provided a panoramic view (Askew, 1985) of shelf edge reefs and their fishes.

Results

Vermilion snapper was very abundant in trawl catches. Although it was relatively infrequent at inner shelf stations (mean catch per tow of 12.4), vermilion snapper was very abundant at middle (243.7 per tow) and outer shelf (140.1 per tow) stations.

Approximately 115 species of prey were identified in 255 stomachs that contained food. Fish with stomachs containing food were found at all times of the day; 22% of stomachs with food were collected between 0001 and 0600 hours local time; 17%, between 0601 and 1200 hours; 18%, between 1201 and 1800 hours; and 43%, between 1801 and 2400 hours. Although no attempt was made in the field to quantify proportions of stomachs with food, there were more stomachs with obvious contents at night (1801–0600 hr).

Most prey items found in vermilion snapper stomachs were planktonic or nektonic organisms (Table 1). Amphipods, mainly planktonic hyperiids and caprellids (e.g., *Lestrigonus bengalensis*, *Phtisica marina*), copepods, and decapods (e.g., larval forms, *Lucifer faxoni*) were the most frequently consumed taxa. These small crustaceans were eaten in large numbers by smaller vermilion snapper, but, with the exception of decapods, contributed little to prey volume (Table 2). Mysids, cumaceans, and doliolids were also frequently consumed. The overall diet was dominated volumetrically by squids and fishes.

Significant feeding differences between size classes were detected by the Tyler chi-square feeding heterogeneity index (Table 2). Several groups of crustaceans and fishes demonstrated significant differences in frequency between size classes of vermilion snapper. Decapods were important prey for larger fish but dominated the diet of fish between 50 and 100 mm SL. Small crustaceans, such as copepods, stomatopods and amphipods decreased in relative number and volume in the diet with increasing size of predator, although amphipods remained a frequent food item in all size classes examined. Barnacles and cumaceans varied in relative volume of prey for different size classes, but cumaceans increased in frequency in larger fish. Although squids and fishes were eaten by most size classes, they were volumetrically most important in

Table 1

Food items that occurred with a frequency (*F*) of at least one percent of stomachs with food, or that made up at least one percent of the total number (*N*) or volume (*V*) of food in vermilion snapper (*Rhomboplites aurorubens*) stomachs (*n*=255). All higher taxonomic groupings of prey are listed, regardless of their frequency, number, or volume. P=planktonic, H=holoplanktonic, D=demersal zooplankton; B=benthic, E=epifaunal, I=infaunal; N=nektonic.

Taxon and prey item	*F*	*N*	*V*
Cnidaria			
nematocysts	1.2	0.1	0.1
Annelida			
Total Polychaeta	11.9	1.8	2.5
Phyllodoce longipes (I)	3.2	0.4	0.3
Mollusca			
Total Gastropoda	5.1	0.9	0.3
Natica pusilla (B)	1.6	0.4	0.1
Total Pelecypoda	1.2	0.3	<0.1
Ervilia concentrica (I)	1.2	0.3	<0.1
Total Cephalopoda	5.9	0.4	43.8
Loliginidae undet.	4.4	0.3	22.4
Loligo plei (N)	0.8	<0.1	21.1
Crustacea			
Total Ostracoda	12.6	11.1	0.2
Ostracoda A (H)	11.1	11.0	0.2
Total Copepoda	43.5	13.4	0.5
Calanopia americana (D)	2.8	0.5	<0.1
Candacia curta (P)	2.8	0.4	<0.1
Centropages furcatus (H)	4.0	0.3	<0.1
Labidocera aestiva (P,B)	6.3	0.7	0.1
Labidocera sp. (H)	1.6	0.2	<0.1
Oncaea sp. (H)	1.6	0.3	<0.1
Sapphirina sp. (H)	1.2	0.1	<0.1
Temora stylifera (H)	9.5	1.6	<0.1
Temora turbinata (H)	21.7	5.3	0.2
Undinula vulgaris (H)	3.2	0.6	<0.1
Total Cirripedia	16.2	3.1	2.5
Barnacle larvae (D)	15.4	3.0	2.5
Total Stomatopoda	9.9	2.2	1.0
Stomatopod larvae (P)	8.3	2.0	0.8
Stomatopoda adults (D)	1.2	0.1	0.2
Total Mysidacea	16.6	5.2	0.8
Anchialina typica (D)	1.2	0.1	<0.1
Bowmaniella portoricensis	9.9	1.0	0.3
Bowmaniella sp.	1.2	0.1	<0.1
Mysidopsis bigelowi (B)	1.2	0.1	<0.1
Promysis atlantica (P)	2.0	3.6	0.4
Total Cumacea	14.6	7.4	1.1
Cyclaspis varians (D)	5.5	0.7	0.1
Oxyurostylis smithi (D)	11.1	5.9	0.8
Total Isopoda	2.0	0.2	<0.1
Total Amphipoda	47.4	13.7	1.8
Gammaridea			
Ampelisca abdita (D)	1.2	0.1	<0.1
Ampelisca vadorum (D)	2.0	0.1	0.1
Corophiidae undet.	1.6	0.3	<0.1
Gammaropsis sp.	2.0	0.2	<0.1
Lysianopsis alba	1.6	0.1	<0.1
Photis sp.	1.2	0.1	<0.1
Rudilemboides naglei	2.0	0.3	<0.1
Synchelidium americanum	1.6	0.1	<0.1
Tiron tropakis	2.0	0.1	<0.1
Caprellidea			
Caprellidae undet.	1.6	0.1	<0.1
Phtisica marina (P,B)	14.6	2.4	0.3
Hyperiidea			
Euprone sp. (H)	1.2	0.1	<0.1
Hyperiidae undet. (H)	5.1	0.5	0.1
Hyperiidea undet. (H)	5.9	0.7	<0.1
Lestrigonus bengalensis (H)	17.8	4.1	0.2
Lycaea sp. (H)	1.2	0.1	<0.1
Phronima sp. (H)	2.0	0.7	0.3
Phronima sedentaria (H)	1.6	0.3	<0.1
Phronimella elongata (H)	2.0	0.8	<0.1
Simorhynchotus sp. (H)	1.6	0.2	<0.1
Total Decapoda	56.5	20.8	11.7
Decapoda undet. zoea (P)	3.2	0.2	<0.1
Decapoda undet. larvae	2.0	0.2	<0.1
Natantia undet. zoea (P)	2.4	0.3	<0.1
Natantia undet. shrimp	12.2	1.3	1.4
Penaeidea			
Lucifer faxoni (H)	14.2	8.5	0.8
Penaeidae zoea (P)	1.2	0.1	<0.1
Sicyonia typica	1.2	0.1	2.0
Solenocera atlantidis	1.2	0.1	0.2
Caridea			
Caridea undet. shrimp	1.2	0.1	<0.1
Leptochela sp.	3.2	0.3	0.2
Leptochela papulata	16.6	2.2	3.0
Ogyrides sp.	2.0	0.2	0.2
Processa sp.	1.2	0.1	0.1
Anomura			
Albunea parettii	4.7	1.4	0.2
Ranilia muricata zoea (P)	2.0	0.2	<0.1
Brachyura			
Brachyura undet. zoea (P)	4.0	0.4	<0.1
Brachyura undet. megalopae (P,B)	7.9	1.1	0.2
Brachyura undet. crab	5.5	0.4	0.4
Calappidae zoea (P)	2.0	0.2	0.1
Ovalipes sp. (P,B)	1.2	0.1	0.4
Pinnotheridae zoea (P)	2.4	0.3	<0.1
Portunidae megalopae (P,B)	4.4	0.6	0.1
Portunidae crab (P,B)	2.8	0.2	0.2
Portunus sp. (P,B)	2.0	0.2	0.2
Xanthidae crab (B)	1.6	0.1	0.3
Sipunculida (B)	1.2	0.1	<0.1
Chaetognatha (P)	13.8	1.9	0.3
Chordata			
Thaliacea			
Doliolida undet. (H)	8.3	7.4	1.2
Larvacea	0.8	<0.1	<0.1
Cephalochordata			
Branchiostoma caribbaeum (D)	3.2	0.4	0.1
Total Teleostei	27.7	6.9	32.2
Anguilliformes	0.4	<0.1	1.3
Prionotus sp. larvae (P)	1.2	4.2	2.6
Sardinella aurita (N)	1.6	0.2	12.4
Teleostei undet. eggs (P)	2.0	3.0	<0.1
Teleostei undet. larvae (P)	3.2	0.4	0.6
Teleostei undet.	14.2	1.3	14.7

Table 2

Percent frequency occurrence (*F*), percent number (*N*), and percent volume (*V*) of higher taxonomic groups of food in the diet of vermilion snapper (*Rhomboplites aurorubens*), by length interval. An asterisk (*) indicates significant differences in prey frequency between one length interval and the adjacent larger interval, based on Tyler's (1979) test.

	Length intervals (mm SL)											
	1–50			51–100			101–150			>150		
Prey	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Cnidaria (nematocysts)	—	—	—	—	—	—	2.9	0.3	0.9	—	—	—
Annelida												
Polychaeta	7.1*	1.6	2.1	10.9	0.4	2.8	13.3	2.2	2.8	10.9	1.6	2.2
Mollusca												
Gastropoda	7.1	0.9	0.2	1.8	0.1	<0.1	5.7	1.6	1.0	6.0	1.4	0.1
Pelecypoda	—	—	—	—	—	—	2.9	1.2	0.2	—	—	—
Cephalopoda	—	—	—	1.8	0.1	1.0	4.8	0.6	24.2	13.4	1.0	51.4
Crustacea												
Ostracoda	28.6	3.7	1.5	24.4*	29.1	3.6	7.6	1.0	0.1	3.0	0.2	<0.1
Copepoda	82.1	33.9	12.0	60.0	15.3	4.0	41.0*	13.1	1.0	16.4	1.9	<0.1
Cirripedia	21.4	6.1	4.2	20.0	1.3	0.5	11.4	2.6	2.5	18.0	4.8	2.6
Stomatopoda	25.0	2.8	9.6	20.0*	4.6	8.4	3.8	0.4	1.5	4.5	0.3	0.3
Mysidacea	21.4	1.9	4.6	12.3	0.7	0.5	20.0	16.0	4.0	11.9	1.5	0.1
Cumacea	3.6	0.9	0.8	7.3*	0.4	0.4	21.0	21.7	5.0	14.9	4.3	0.3
Isopoda	3.6	0.2	0.2	—	—	—	—*	—	—	6.0	0.5	0.1
Amphipoda	35.7	20.3	12.7	49.1	12.9	6.2	49.5	14.2	4.0	46.3	11.5	0.9
Decapoda	35.7*	25.0	31.1	70.9*	29.4	42.0	52.4	14.1	19.0	58.2	14.3	7.9
Sipunculida	—	—	—	—	—	—	1.9	0.2	0.1	1.5	0.1	<0.1
Chaetognatha	21.4	1.6	3.4	10.9	1.3	0.9	11.4	2.3	0.8	16.4	2.3	0.1
Chordata												
Thaliacea	3.6	0.2	0.4	9.1	1.5	1.6	5.7	2.0	0.4	13.4	24.9	1.3
Larvacea	—	—	—	—	—	—	—	—	—	3.0	0.2	<0.1
Cephalochordata	—	—	—	1.8	0.1	0.2	2.9	1.0	0.2	6.0	0.4	0.1
Teleostei	7.1*	0.7	17.1	43.6*	2.9	27.8	21.9*	5.5	32.4	38.8	28.8	32.7
Examined stomachs with food:	28			55			105			67		
Mean SL (mm) of fish with food:	36.4			77.8			131.1			168.1		

the diet of larger vermilion snapper (Table 2). Squids and fishes were 76% of the prey volume for all vermilion snapper, but 84.1% of the prey volume (and only 29.8% by number) of fish greater than 150 mm SL.

Vermilion snapper fed sparingly on invertebrates closely associated with the reef habitat and collected in suction and grab samples during the day (Table 3). Electivity values were negative (usually –1.00) for all dominant species in benthic samples. Polychaete species that dominated those samples consisted mainly of tube-reef building species (*Filograna implexa*) and species associated with sponges and corals (*Exogone dispar* and *Syllis spongicola*) (Gardiner, 1975; Wendt et al., 1985); none of these were consumed by vermilion snapper. On the other hand, many species that dominated numerically in the diet (e.g., *Oxyurostylis smithi* and *Lucifer faxoni*) were collected in benthic samples but were not a major component of the daytime reef fauna. Because abundance of these species in benthic samples was so low, electivity values were positive. Those species that were higher in relative abundance in stomachs than in benthic samples (e.g., *O. smithi*) may have been consumed in the water column during periodic emergence.

As in the case of benthic samples, most species of cumaceans, mysids, stomatopods, and decapods that dominated samples from the sled were not as relatively abundant in stomach samples (Table 4). Most electivity values were negative; however, fewer absences from stomach samples (E=–1.00) occurred with the dominant species from sled samples than with the benthic samples. The mysid *Promysis atlantica* at the inner shelf (E=0.77) and the decapod *Lucifer faxoni* at the middle shelf (E=0.63) were dominant species in sled samples that were positively elected as prey. *Lucifer faxoni* was by far the most abundant species in

Table 3

Relative abundance (percent of total number of individuals, N) and electivity values (E) for dominant benthic species in suction and grab samples and in vermilion snapper (*Rhomboplites aurorubens*) stomachs. Dominant species for each type of sample (benthic or stomach) include those that ranked in the five most abundant species in any depth zone for that type of sample.

	Inner shelf			Middle shelf			Outer shelf		
	Relative abundance			Relative abundance			Relative abundance		
	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E
Dominant species — benthic samples									
Chone americana	—	0.33	–1.00	—	0.81	–1.00	—	0.59	–1.00
Erichthonius brasiliensis	0.09	2.89	–0.94	—	0.30	–1.00	—	0.13	–1.00
Erichthonius sp. A	—	0.08	–1.00	—	—	—	—	3.75	–1.00
Exogone dispar	0.44	3.71	–0.79	—	0.47	–1.00	—	0.01	–1.00
Filograna implexa	—	20.42	–1.00	—	63.87	–1.00	—	21.90	–1.00
Luconacia incerta	—	3.27	–1.00	0.05	1.03	–0.90	—	0.18	–1.00
Malacoceros glutaeus	—	0.41	–1.00	—	0.81	–1.00	—	0.02	–1.00
Phyllochaetopterus socialis	—	0.21	–1.00	—	0.12	–1.00	—	12.40	–1.00
Pista palmata	—	0.09	–1.00	—	0.08	–1.00	—	8.60	–1.00
Podocerus sp. A	—	2.87	–1.00	—	0.27	–1.00	—	0.14	–1.00
Spiophanes bombyx	—	0.39	–1.00	—	0.46	–1.00	—	5.81	–1.00
Syllis spongicola	—	2.14	–1.00	—	1.90	–1.00	—	1.38	–1.00
Total	0.53	36.81		0.05	70.12		0.00	54.92	
Dominant species — stomachs									
Bowmaniella portoricensis	0.18	0.09	0.32	1.80	0.10	0.89	0.50	0.22	0.37
Leptochela papulata	0.35	0.04	0.81	3.45	0.09	0.95	1.86	0.12	0.88
Lucifer faxoni	12.05	0.18	0.97	9.79	0.01	0.99	0.62	0.04	0.87
Oxyurostylis smithi	15.74	0.67	0.92	2.46	0.14	0.89	—	—	—
Phtisica marina	0.09	0.01	0.75	1.80	0.03	0.97	7.20	0.40	0.90
Phyllodoce longipes	1.14	0.06	0.89	0.05	0.04	0.10	0.12	0.20	–0.22
Promysis atlantica	11.79	—	1.00	0.05	<0.01	0.88	—	—	—
Rhudilemboides naglei	1.06	0.05	0.91	—	<0.01	–1.00	—	0.04	–1.00
Total	42.40	1.10		19.40	0.42		10.30	1.02	
Number of stomachs with food:		49			138			68	

sled samples at the inner shelf and was also abundant in stomach samples but demonstrated negative electivity at the inner (E=–0.53) and outer (E=–0.39) shelf sites. At the middle shelf, *L. faxoni* was the most abundant species in the analyzed taxa in fish stomachs and ranked third in abundance in sled samples. Many of the species that were high in relative abundance in fish stomachs also occurred in sled samples; however, electivity values were not always positive. The relative abundance of cumaceans, mysids, stomatopods, and decapods in fish stomachs, compared with their abundance in sled samples, indicated that vermilion snapper often selected crustaceans in higher proportions than was their availability to the plankton sled at night (Table 4). Included were several orders of Crustacea, particularly the cumacean *Oxyurostylis smithi* and the mysid *Promysis atlantica* at inner shelf stations, the decapods *Lucifer faxoni* and *Leptochela papulata* at middle shelf stations, and the decapods *Leptochela papulata* and *Solenocera atlantidis* at the outer shelf.

Comparing dominant species in the diet of vermilion snapper with their relative abundance in benthic (lower half of Table 3) and sled (lower half of Table 4) samples indicated high positive selectivity for most prey species from both environments sampled. For suction and grab samples, this was due to the extremely low abundance (<1%) of all the dominant prey in the benthos. For the sled samples, many dominant prey species were also dominant in the environment.

Discussion

The vermilion snapper is well adapted to foraging in the water column (Davis and Birdsong, 1973; Grimes, 1979). Grimes (1979) reported that the diet of vermilion snapper was dominated by planktonic organisms

Table 4

Relative abundance (percent of total number of individuals, *N*) and electivity values (*E*) for dominant species of decapods, cumaceans, mysids and stomatopods in sled samples and vermilion snapper (*Rhomboplites aurorubens*) stomachs. Dominant species for each type of sample (sled or stomach) include those that ranked in the five most abundant species of decapods, cumaceans, mysids and stomatopods in any depth zone for that type of sample.

	Inner shelf			Middle shelf			Outer shelf		
	Relative abundance			Relative abundance			Relative abundance		
	Fish stomachs	Sled samples	*E*	Fish stomachs	Sled samples	*E*	Fish stomachs	Sled samples	*E*
Dominant species — sled samples									
Bowmaniella portoricensis	0.30	5.56	−0.90	5.52	10.45	−0.31	4.30	5.45	−0.12
Lucifer faxoni	20.57	66.77	−0.53	29.93	6.79	0.63	5.38	12.29	−0.39
Mysidopsis furca	—	0.67	−1.00	0.17	4.49	−0.93	—	22.28	−1.00
Neopontonides beaufortensis	—	4.10	−1.00	—	3.35	−1.00	—	0.77	−1.00
Periclimenes iridescens	—	3.18	−1.00	—	3.75	−1.00	—	0.84	−1.00
Pontophilus gorei	—	—	—	—	0.03	−1.00	—	7.33	−1.00
Promysis atlantica	20.12	2.57	0.77	0.17	7.24	−0.95	—	0.63	−1.00
Thor manningi	—	0.05	−1.00	—	0.43	−1.00	—	2.44	−1.00
Total	40.99	82.90		35.15	36.63		9.68	52.03	
Dominant species — stomachs									
Bowmaniella portoricensis	0.30	5.56	−0.90	5.52	10.45	−0.31	4.30	5.45	−0.12
Cyclaspis varians	1.05	0.05	0.91	3.18	1.45	0.37	—	0.41	−1.00
Lucifer faxoni	20.57	66.77	−0.53	29.93	6.79	0.63	5.38	12.29	−0.39
Leptochela papulata	0.60	0.39	0.21	10.54	2.07	0.67	16.13	1.61	0.82
Oxyurostylis smithi	26.88	1.38	0.90	7.52	1.19	0.73	—	0.42	−1.00
Promysis atlantica	20.12	2.57	0.77	0.17	7.24	−0.95	—	0.63	−1.00
Solenocera atlantidis	—	—	—	—	0.03	−1.00	4.30	1.12	0.59
Total	69.52	80.82		56.86	32.56		30.11	22.70	
Number of stomachs with food:		49			138			68	

and he noted that the diet of juveniles (<100 mm TL) was dominated volumetrically by copepods. In the present study, decapods dominated the diet volume of fish less than 101 mm SL. The feeding habits of vermilion snapper changed considerably with size in the present study, although pelagic prey dominated in all size classes. As vermilion snapper grows, it switches from a diet of many small crustaceans, to a diet dominated by a few large cephalopods, fishes, or decapod crustaceans. The switch to different prey taxa and to fewer, larger prey individuals was similar to ontogenetic diet changes noted by Sedberry (1983) for several demersal fishes from the outer continental shelf. In contrast, Schmitt and Holbrook (1984) found that black surfperch (*Embiotoca jacksoni*) switched to larger prey, but that gross taxonomic composition of the diet did not change and that surfperch continued to feed on macrocrustaceans, in spite of growth and changes in body size and foraging behavior. Vermilion snapper, like many other fishes (Sedberry, 1983), apparently becomes capable of taking larger prey as it grows and switches from picking plankton to pursuing and capturing active nektonic species, such as Spanish sardine (*Sardinella aurita*), and squids.

Grimes (1979) suggested that vermilion snapper is a nocturnal forager and that selective feeding by vermilion snapper on demersal zooplankton, such as cumaceans, indicates nocturnal foraging. These crustaceans are infaunal in the sand or epifaunal in reef crevices during the day but emerge at night (Anger and Valentin, 1976; Alldredge and King, 1985), becoming prey for vermilion snapper and other fishes that forage on near-bottom zooplankton at night. Demersal zooplankton demonstrating nocturnal emergence and found in the diet of vermilion snapper included syllid polychaetes, some calanoid copepods, cumaceans, amphipods, decapods, barnacle and stomatopod larvae, chaetognaths and cephalochordates (Williams and Bynum, 1972; Fincham, 1974; Anger and Valentin, 1976; Hobson and Chess, 1976; Alldredge and King, 1977; Hammer, 1981; Alldredge and King, 1985; Cahoon and Tronzo, 1988). These taxa are dominant members of the demersal zooplankton (Porter and Porter, 1977) and emerge from benthic habitats at night when they

feed, molt, reproduce or disperse (Alldredge and King, 1985). This behavior makes them subject to intense predation by vermilion snapper or other specialized nocturnal predators (Robertson and Howard, 1978).

Demersal zooplankton are approximately as abundant as holozooplankton on the continental shelf off North Carolina (Cahoon and Tronzo, 1992), and the nocturnal emergence of demersal zooplankton probably increases overall food availability at night, while allowing planktivorous fishes to feed under the cover of darkness. Small vermilion snapper are prey for diurnal lutjanids and crepuscular serranids (South Carolina Wildlife and Marine Resources Department[1]; Parrish, 1987; Sedberry, 1988) and would be subject to predation during the day.

Vermilion snapper also consumes holoplanktonic species such as copepods, hyperiids, *Lucifer faxoni*, and doliolids, as well as nektonic squids and fishes. As noted by Grimes (1979), squids were especially important in the diet of large juveniles and adults. These larger size classes of vermilion snapper also fed more on fishes, which included schooling pelagic species such as Spanish sardine, *Sardinella aurita*. Spanish sardine makes up 9.4% of fishes caught in trawls on the southeastern continental shelf[2]. Predation by vermilion snapper on nektonic foragers such as squids and Spanish sardine provides a trophic link between the pelagic nekton and the reef. In the role as an abundant consumer of nekton, holoplankton, and demersal zooplankton, vermilion snapper may be important in transferring energy from benthic sand habitats and the water column to the reef, in the form of feces. Feces that disintegrate just above the reef provide fine particles and nutrients for filter- and suspension-feeders, and fecal pellets that are less refractile can be used directly by small crustaceans and other organisms living in the reef (Rothans and Miller, 1991). Vermilion snapper appear to be relatively inactive during the day, hovering or moving slowly in large schools along the reefs within a meter of the bottom (pers. observ. by GRS from *Sea Link I*). By feeding in the water column at night and swimming just above the reef during the day, vermilion snapper enhances the transfer of this organic matter to the benthos. During these diurnal resting periods, vermilion snapper probably deposit feces, derived from water column nocturnal foraging, onto the reef. Bray et al. (1981) also found that a planktivorous reef fish functioned as a trophic link between the plankton and benthos by importing organic carbon to the reef in the form of feces. Meyer and Schultz (1985) found that grunts (*Haemulon* spp.) feeding on sand flats transferred significant amounts of nutrient and organic matter to reefs, thus enhancing coral growth.

Benthic polychaetes ranking high in relative abundance in the suction and grab samples were not important in the diet of vermilion snapper, and electivity values for all dominant species in the benthic samples were negative. The dominant crustaceans in benthic samples were epibenthic species such as the corophoid amphipod, *Erichthonius brasiliensis*, and the caprellid amphipod *Luconacia incerta* which attach to sessile invertebrates and are usually closely associated with the reef substratum (McCain, 1968; Bousfield, 1973). Because *E. brasiliensis* and caprellid amphipods have also been found in nocturnal zooplankton samples (Williams and Bynum, 1972; Hobson and Chess, 1976), they may be consumed by predators at night in the water column. Some motile benthic crustaceans such as mysids, cumaceans, and decapods that were common in vermilion snapper stomachs were much higher in relative abundance in stomachs than in benthic samples. Vermilion snapper apparently prey on these benthic crustaceans during their periodic migrations into the water column. The polychaetes that dominated benthic samples apparently do not undertake such migrations.

Vermilion snapper feed on many of the same prey species as the benthic-feeding sparid *Stenotomus chrysops*, an abundant demersal fish of the continental shelf (Sedberry and Van Dolah, 1984; Sedberry, 1988; Sedberry et al.[2]). Submersible observations indicate that *S. chrysops* feeds during the day on the benthos, living in sand adjacent to reef habitat, whereas vermilion snapper were not observed to forage in this manner. Vermilion snapper apparently consumes sand-dwelling benthos at night, when they emerge from the bottom, while *S. chrysops* feeds on benthos during the day when demersal zooplankton has burrowed in the bottom. This provides a temporal partitioning of prey resources between these two dominant species of reef-associated fish.

For reef fishes of the southeastern shelf, there is large variation in the degree of dependence on hard substrate as a habitat for prey (Sedberry, 1985, 1987, 1988). Of the three most abundant species in our reef trawl catches (*S. chrysops*, *Haemulon aurolineatum*, and *R. aurorubens*), all occur over sand bottom, although they are much more abundant over reefs (Wenner, 1983; Sedberry and Van Dolah, 1984). The

[1]South Carolina Wildlife and Marine Resources Department. 1984. Final Report. South Atlantic OCS area living marine resources study. Phase III. Volume 1. Prepared by Marine Resources Research Institute, SCWMRD, for Minerals Management Service, Washington, D.C., under contract No 14-12-0001-29185, 223 p.

[2]Sedberry, G. R., C. A. Barans, C. A. Wenner, and V. G. Burrell Jr. The ichthyofauna of sandy bottom habitat on the continental shelf off the southeastern U.S. Manuscr. in prep.

former two species feed primarily on sand bottom benthos (Sedberry, 1985, 1988). Although *H. aurolineatum* and *S. chrysops* feed heavily on sand infauna and are not completely dependent on reef habitat, vermilion snapper is more restricted to reef habitat and does not range far from a home reef (Fable, 1980). Wenner (1983) collected only 2 specimens in 11 trawling tows in sand bottom habitat on the southeastern continental shelf, whereas *S. chrysops* and *H. aurolineatum* are dominant species in sand habitats (Wenner, 1983; Sedberry[2]). Vermilion snapper did not, however, feed directly on reef fauna, and its attraction to reefs may be behavioral rather than trophic.

Although vermilion snapper feeds extensively on demersal zooplankton, many individuals also feed opportunistically on concentrations of holoplankton that occur on the southeastern shelf. Copepods, such as *Undinula vulgaris* and especially *Temora turbinata*, that were frequent food items for vermilion snapper are epipelagic oceanic species that are transported landward across the continental shelf (Hopkins et al., 1981). Off the southeastern United States, upwelling at the shelf edge and cross-shelf transport of deep, highly productive oceanic water provide mechanisms for shoreward movement of shelf-edge biota, including copepods (*U. vulgaris*, *T. turbinata*, *Oncaea* spp.), doliolids, sergestid decapods (e.g., *Lucifer faxoni*), and other abundant oceanic zooplankters (Yoder et al., 1983; Paffenhöfer et al., 1984). Vermilion snapper, one of the most abundant fishes at shelf edge depths (Sedberry and Van Dolah, 1984), apparently takes advantage of this abundant resource and performs the function of transferring some of this oceanic productivity to bottom habitats on the continental shelf.

In conclusion, vermilion snapper feeds on a variety of prey above the substrate, much of which is demersal zooplankton. Although it is unknown how much of the biomass of the daytime benthos is composed of nocturnally emerging demersal zooplankton, it is apparent that these organisms are an important food source for vermilion snapper and other reef fishes. Demersal zooplankton, such as mysids, cumaceans, ampeliscid amphipods, and certain decapods, composed at least eight percent of the total volume of food for vermilion snapper in the present study and are more important in the diet of smaller size classes. While a small contribution, these benthic species provide a feeding opportunity for vermilion snapper and may be more important in the diet during periods of low productivity of holoplankton. Nektonic fishes and cephalopods provide the greatest volume of food for larger vermilion snapper. Because it is prey for other reef predators, vermilion snapper is an important trophic link among several habitats on the southeastern continental shelf.

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Latitudinal variation in the birth timing of captive California sea lions and other captive North Pacific pinnipeds

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Abstract.—The relationship between latitude and birth timing was assessed for captive-born California sea lions (*Zalophus californianus*), northern (Steller) sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), and Pacific harbor seals (*Phoca vitulina richardsi*) from zoos and aquaria in the United States, Canada, South Korea, and New Zealand. The births of 466 viable California sea lion pups demonstrated highly significant, negative and curvilinear latitudinal variation in birth timing. Over the latitudinal range of captive births, this variation accounted for a change of approximately –0.6 days/°latitude. Furthermore, the variances of the mean dates of birth for the largest 18 captive populations were significantly dependent upon latitude; shorter birthing periods occurred at higher latitudes. Northern sea lions (n=9) had a similar, but non-significant latitudinal relationship in which birthing dates occurred approximately 30 days later. No significant relationship between latitude and birthing date was found for northern fur seals (n=13). The birth dates of 110 viable Pacific harbor seal pups had highly significant, positive and curvilinear latitudinal variation, similar to that previously described for this subspecies in the wild between 30° and 47°N. Pupping dates for each species in captivity were comparable to those found for wild populations of North Pacific pinnipeds. The described latitudinal variation and the temporal consistency between captive and wild populations of California sea lions and Pacific harbor seals support the hypothesis that photoperiod response maintains specific birth timing in these species.

Captive pinnipeds are not only of educational and entertainment value to zoo and aquarium visitors, but also offer an exceptional opportunity to examine temporal aspects of their reproductive biology. Zoo records usually document birth dates, outcomes, and parental histories which are difficult, if not impossible, to obtain in field studies. Moreover, captive animals live in environments where availability of food is relatively constant and any movements (i.e., transfers between facilities) are well documented.

A recent census (Asper et al., 1988) identified 924 pinnipeds in captivity in North America. Of these, four North Pacific species—the California sea lion (*Zalophus californianus*), the northern or Steller sea lion (*Eumetopias jubatus*), the northern fur seal (*Callorhinus ursinus*), and the harbor seal (*Phoca vitulina*)—represented 91 percent (n=837). These species breed successfully in captivity over wide latitudinal ranges.

Standard reviews of the pinnipedia (Mate, 1979; Mate and Gentry, 1979; Odell, 1981; Schusterman, 1981; King, 1983) identify fixed seasons of birth for each of the North Pacific sea lions. Moreover, Bigg (1973) found that captive California sea lions at the London Zoo (51°N) breed at the same time as the parent population in California (33°N). In contrast, Schusterman et al. (1982) noted that births of California sea lion pups at Sea Life Park, Hawaii (21°N), occurred significantly later than births in California at Marineland (34°N) and Marine World (38°N).

Regional or latitudinal variation in birth timing, or both, has been reported for the harbor seal (Bigg, 1969a; Temte et al., 1991) and the grey seal (*Halichoerus grypus*: Coulson, 1981). Likewise, Temte (1985) demonstrated a 14-day shift in the mean date of pupping for northern fur seals between colonies on St. George Island, Alaska (57°N), and San Miguel Island, California (34°N). These variations in birth timing have been interpreted as 1) selection acting on discrete populations to match reproductive efforts with seasonal constraints (Bigg, 1973), 2) responses to latitudinally changing temporal cues, such as temperature or photoperiod (Coulson, 1981; Temte, 1985), or 3) a combination of the above (Temte et al., 1991; Boyd, 1991).

This study identifies and defines the extent of latitudinal variation in birth timing of captive California sea lions, northern sea lions, northern fur seals and Pacific harbor seals from birthing records available from zoos and aquaria scattered across a wide latitudinal range. Comparisons of birthing periods were made, where applicable, between captive and wild populations.

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Methods

The data

Data for this analysis were initially compiled from the Marine Mammal Inventory Report (MMIR), a registry of captive marine mammals maintained by the Office of Protected Resources, National Marine Fisheries Service. To comply with the Marine Mammal Protection Act, U.S. facilities that exhibit marine mammals submit yearly summaries of their captive populations, including animal identification, sex, age, date of acquisition or birth, origin, and current status. The birth dates of 527 California sea lions born in captivity at 41 locations, 9 northern sea lions born at two locations, 20 northern fur seals born at three locations, and 125 Pacific harbor seals born at 13 locations were extracted from this registry (Fig. 1). Seventy-one percent of birth date and outcome (viable pup, non-viable pup, stillborn pup) data were independently verified by contacting the appropriate facility. Of the data verified, 98.6% were accurately reported on the MMIR (Temte, 1993).

Eighty-three additional captive births of California sea lions, not reported on the MMIR, were provided by the facilities. Seven additional birth dates of captive northern fur seals were obtained from the report of Bigg (1984). Data on two births of harbor seals were obtained from the Vancouver Aquarium (Vancouver, British Columbia). To assess the effect of a major latitudinal translocation, birthing dates of 11 California sea lions born at the Auckland Zoo, New Zealand (37°S) were obtained. All cows at this facility could be traced, from zoo records, to the California Channel Islands population.

Pup identification, location, latitude, date of birth, sex, and birth outcome were entered into the database. Dates of birth were converted into numerical equivalents by using a sequential astronomical calendar (day 0 = December 21; see Temte, 1985). Birth outcomes were rated as stillbirth (pup born dead), non-viable (pup lived less than one day), or viable (pup lived at least one day).

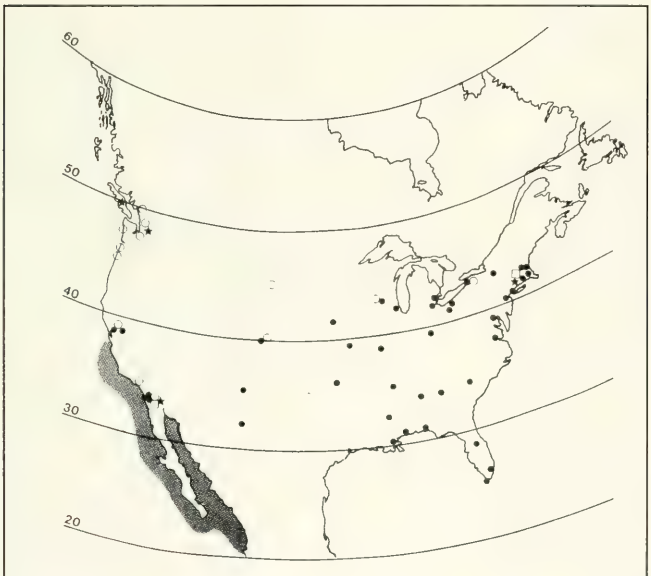

Figure 1

Locations of zoos, aquaria and marine zoological parks where captive births of California sea lions (filled circles), northern sea lions (open boxes), northern fur seals (stars) and Pacific harbor seals (open circles) have been reported. Sea Life Park, Waimanalo, Hawaii (21°20'N: CSL), Auckland Zoo, Auckland, New Zealand (37°52'S: CSL) and Seoul Grand Park, Seoul, South Korea (37°31'N: PHS) are not shown. The shaded area indicates the natural breeding range of the California sea lion.

Statistical analysis

Data were treated separately for each species. Comparisons were made between the mean dates of birth for stillborn, non-viable, and viable pups by using the appropriate parametric or non-parametric statistic.

The birth dates of viable pups were assessed for latitudinal variation. Least squares linear regression models were fitted to the latitude-date data, and where necessary, orthogonal polynomials were used to meet statistical assumptions. Because the intra-colony variance of the mean date of birth for California sea lions was related to latitude, regressions were performed with and without weighting to correct for unequal variances. Orthogonal polynomial regression models using (latitude minus mean latitude)^2 as the quadratic term were chosen to reduce correlation between the linear and quadratic terms and to better estimate the linear coefficient (Snedecor and Cochran, 1980). To assess differences between California and northern sea lions, analysis of covariance (ANCOVA: Kleinbaum and Kupper,

1978) was utilized to control for differences in latitudinal distributions.

Results

California sea lion

The captive births of 610 California sea lions were evaluated (Table 1). Stillborn and non-viable pups accounted for 122 births (20.0%). Stillbirths occurred as early as 1 January and as late as 1 August. Whereas no significant difference was found between the timing of stillbirths and non-viable births (Kruskal-Wallace: df=1; H=0.371; NS), stillborn and non-viable pups were born an average of 28.0 days earlier than viable pups, this difference being highly significant (Kruskal-Wallace: df=1; H=70.49; P<0.001). Hence, only viable births (n=466; 22 pups with estimated birth dates were excluded) were examined for latitudinal variation.

Viable births occurred over a 21°46' latitudinal range, between 21°20'N and 43°06'N. These were normally distributed over the birthing period (Fig. 2), occurring as early as 30 April and as late as 1 September. Mean dates of pupping for individual colonies occurred from 27 May to 25 June. The mean date of birth for all viable pups was 12 June ± 13.5 days (± SD).

The variances of the mean birth dates were calculated for the 18 largest captive colonies (each with at least 6 viable births). A significant latitudinal gradient existed for this variance (Fig. 3), with a decrease of 5.6 days^2 for each degree of northward displacement.

A plot of pupping date versus latitude indicated that latitude variation occurred within captive California sea lions (Fig. 4). A second order orthogonal polynomial model (Table 2) was highly significant (r^2=0.206; $F_{[2,463]}$=60.23; P<0.0001) and estimated a negative latitudinal slope of approximately –0.6 days/°latitude over

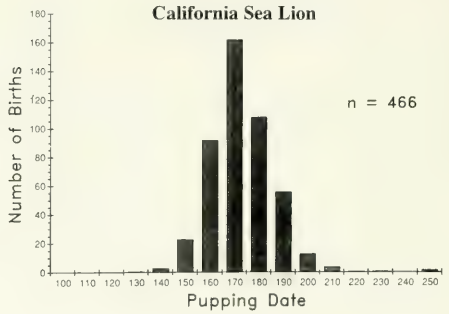

Figure 2

Frequency of viable California sea lion births at all facilities during 10-day periods from 31 March (day 100) to 6 September (day 259). Dates are numbered sequentially from 21 December.

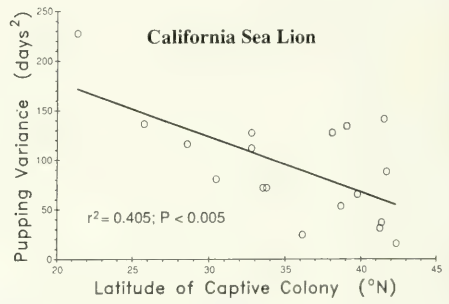

Figure 3

Intra-colony variance of the mean pupping date from the 18 largest California sea lion colonies as a function of latitude. Each colony had at least six viable births. Linear regression model: Variance (days^2) = 219 – 5.58(latitude); r^2 = 0.405; t_{slope} = –3.30; P < 0.005.

Table 1

Numbers, mean dates (month/day; sequential day number), and standard deviations of viable births, non-viable births, and stillbirths in captive North Pacific pinnipeds.

Species	Type	n	Percent	Mean date	SD (days)
California sea lion	Viable	488	80.0	6/12 (172.7)	13.5
	Non-viable	50	8.2	5/16 (145.6)	29.4
	Stillborn	72	11.8	5/14 (144.0)	46.1
Northern sea lion	Viable	9	100.0	7/09 (199.8)	16.5
Northern fur seal	Viable	13	48.1	7/10 (200.6)	14.8
	Stillborn	14	51.9	6/23 (184.2)	60.0
Pacific harbor seal	Viable	110	88.0	5/20 (150.3)	36.7
	Non-viable	5	4.0	5/11 (140.8)	47.5
	Stillborn	10	8.0	5/11 (140.8)	34.0

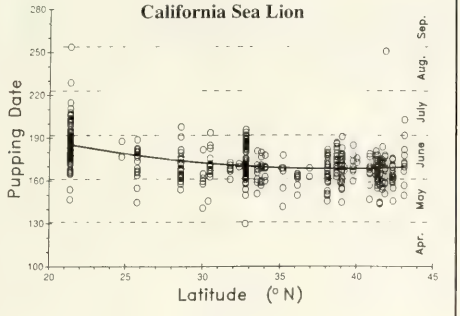

Figure 4
The birth timing of viable California sea lions as a function of latitude. See Table 2 for regression model.

the range of data. Weighting of the regression to correct for the unequal variances did not appreciably change the parameter estimates.

Eleven pups were born at the Auckland Zoo (Auckland, New Zealand: 37°S) from 28 November to 23 December and had a mean birth date of 11 December. The polynomial model predicted that birthing at 37°N should occur on 6 June. Therefore, California sea lions translocated to the Southern Hemisphere experienced an approximate 6-month shift in birth timing.

Climatic conditions did not appear to significantly affect the timing of birth. For example, colonies at similar latitudes (Vallejo, California: 37°47'N and Kansas City, Missouri: 39°07'N) maintained similar pupping schedules despite having vastly different seasonal temperature cycles. Following an adjustment for latitude, no significant difference was found between the birth timing of male and female pups.

Northern sea lion

The captive births of nine northern sea lions occurred at 32°45'N and 41°21'N (latitudinal range=8°36'). All births were of viable pups. The mean date of birth was 9 July ± 16.5 days (± SD; Table 1). Although the plot of pupping date vs. latitude was similar to that for the California sea lion, a simple linear regression model (Table 2) failed to demonstrate significant latitudinal effects in this species (r^2=0.271; $F_{[1,7]}$=2.60; P=0.23); the lack of significance was possibly due to the small sample size. However, when northern sea lion data were combined with those of the California sea lion in a multiple linear regression model, no significant differences were found between the latitudinal slopes of the two species. Analysis of covariance identified significantly later birthing (P<0.001) for northern sea lions, occurring 30 days after California sea lions.

Northern fur seal

The captive births of 27 northern fur seals were reported from four locations between 32°45'N and 49°07'N (latitudinal range=16°22'). Slightly more than half of the pups were stillborn (Table 1). The mean date of birth of viable pups was 10 July ± 14.8 days (± SD). No significant latitudinal variation was detected in birth timing (Table 2: r^2=0.174; $F_{[1, 11]}$=2.32; NS).

Pacific harbor seal

The birth dates of 127 captive-born Pacific harbor seals were identified from 14 locations between 32°45'N and 49°18'N (latitudinal range=16°33'). The birth outcomes of two pups were not known and they were excluded from further analysis. Of the remaining 125 births, 88.0% were of viable pups (Table 1). The mean date of birth for viable pups was 20 May ± 36.7 days (± SD). No significant differences in the annual birth timing

Table 2
Regression models for latitudinal variation in birth timing of North Pacific pinnipeds.

Species	n	Mean latitude (° North)	*Linear regression estimate of $PD = a + b_1(L) + b_2(L - \bar{L})^2$ a	b_1 (CI) ±95%		b_2 (CI) ±95%		r^2	Significance
California sea lion	466	33.21	190	–0.61	(0.17)	0.057	(0.024)	0.206	0.0001
Northern sea lion	9	35.62	271	–2.00	(2.43)	—	—	0.271	NS
Northern fur seal	13	45.03	145	1.23	(1.59)	—		0.174	NS
Pacific harbor seal	110	41.60	–113	5.85	(1.10)	0.681	(0.065)	0.508	0.0001

*PD = Pupping date (sequential from 21 December); L = Latitude.

were found among viable, non-viable and stillborn pups.

A simple linear regression model defined significant latitudinal variation in birth timing of viable pups with a gradient of 4.10 days/°latitude; this slope was not significantly different from that reported by Temte et al. (1991) for colonies of wild Pacific harbor seals between 30° and 47°N. A second order polynomial model (Fig. 5; Table 2), however, was more statistically appropriate based on residual analysis. This model was highly significant (r^2=0.508; $F_{[2,107]}$=55.23; P<0.0001), defining a positive relationship between latitude and birth date.

Data regarding sex of pup (n=102), maternal age (n=88), and the previous annual cycle of the mother (pregnant vs. non-pregnant: n=89) were available for subsets of the harbor seals. When entered, either separately or as a group, into a multiple regression model adjusting for latitude, none of these parameters was found to significantly alter birth timing.

Discussion

Use of captive birth data

Events on rookery sites or pupping beaches hamper the estimation of true pupping seasons in pinnipeds. For example, premature pupping in the California sea lion occurs with increasing frequency over a 5-month period, melting into the normal pupping season between mid-May and the end of June (Delong et al., 1973). In addition, seasonal movements of animals from breeding to feeding sites may occur (Braham, 1974; Mate, 1975), potentially obscuring latitudinal variation of birthing if seasonal entrainment occurs at latitudes other than that of the rookery site. The use of captive populations permits accurate measurement of birth dates and birth outcomes, while controlling for potential latitudinal displacement during the reproductive year.

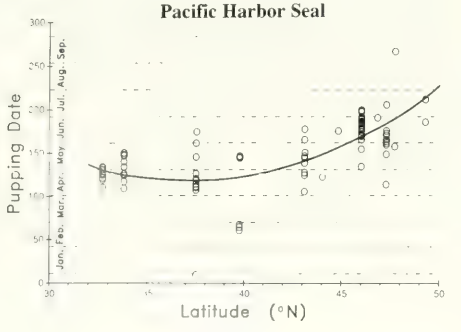

Figure 5
The birth timing of viable Pacific harbor seals as a function of latitude. See Table 2 for regression model.

California sea lion

This study confirms the report of Schusterman et al. (1982) and demonstrates that marked latitudinal variation occurs not only in the timing of birth, but also in the variance of the mean birth date. Furthermore, interpretations of results based on this data set representing 466 viable births from 41 locations, as compared to the three locations used by Schusterman et al. (1982), are far less sensitive to possible confounding effects induced by captivity or differences in climatic conditions. The extreme example of sea lions translocated to the Southern Hemisphere provides further evidence of strong latitudinal effect.

The birth timing of captives mirrors that of wild populations. Although a review by Mate (1979) concluded that pups, regardless of latitude, are born from mid-May to late-June over the range of California sea lion rookeries, slight latitudinal variation may exist. In Baja California, pupping occurs in late-June (Brownell et al., 1974), and Le Boeuf et al. (1983) reported a maximum pup count on 10 July at Los Islotes (28°N). Further to the north, at San Nicolas Island (33°15'N), pupping peaks during the first half of June (Peterson and Bartholomew, 1967; Odell, 1975; Heath and Francis[1,2]). Data from more northerly colonies are anecdotal in nature. For example, Braham (1974) reported a 2-week-old pup on 11 June at San Luis Obispo County, California (35°30'N).

As in captive sea lions, premature pupping in wild colonies occurred as early as January on San Nicolas and San Miguel Islands (Odell, 1970; Delong et al, 1973). Premature pups are probably represented in captivity by the stillborn and non-viable groups. The 20% rate of stillborn and non-viable pupping for captive sea lions is noteworthy considering the 5–16% rate of premature pupping reported for San Nicolas Island during years with high incidences of prematurity (Odell, 1970). Whereas pesticide exposure and disease

[1]Heath, C., and J. Francis. 1983. California sea lion population dynamics and feeding ecology with applications for management. Results of 1981–1982 research on Santa Barbara and San Nicholas Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Center, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-83-04C.

[2]Heath, C., and J. Francis. 1984. Results of research on California sea lions, San Nicholas Island, 1983. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Center, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-84-41C.

have been suggested as agents of premature pupping in wild populations (Delong et al., 1973; Odell, 1970, 1981), the high rate of stillbirth and non-viability in captivity may be influenced by the level of surveillance inherent to captive populations.

Male California sea lions were reported to be 3.37 cm longer and 1.41 kg heavier than female pups at birth (Le Boeuf et al., 1983). Year-to-year differences in mean birth lengths and weights have been related to differences in the mean birth date of harbor seals (Boulva, 1975). No such differences were found between the birth timing of male and female pups in the present study. Hence, discrepancy in birth size is likely due to greater growth velocity of fetal males.

Northern sea lion

Only limited data from two locations were available for captive northern sea lions. Although these animals appeared to have a temporal pattern of birth similar to, but 30 days later than, that of the closely related California sea lion, no significant latitudinal trend was found.

The northern sea lion has a wide distribution of breeding (see Fig. 1 in Loughlin et al., 1984), but little evidence exists for latitudinal variation in birth timing in the wild. For example, a review of median birth dates at rookeries from 37°N to 60°N by Merrick (1987) failed to demonstrate any latitudinal variation in this species.

Northern fur seal

A high rate of stillbirth was noted for the fur seal. This phenomenon was previously reported by Bigg (1984) during studies indicating that contact with substrate (e.g., arrival on shore) may stimulate parturition. Captive environments, with shallow pools and access to platforms, cannot adequately reproduce the pelagic environment which female fur seals inhabit during most of active gestation. Hence, premature parturition may be induced by enclosures.

The mean date of pupping for viable pups in captivity of 10 July was the same as that derived for St. George Island, Alaska (Temte, 1985). Unlike wild northern fur seals, however, the captives demonstrated no significant latitudinal variation. The sample set may have been too small to detect the estimated 0.6 days/°latitude trend reported by Temte (1985).

Pacific harbor seal

Captive harbor seals had a high rate of viable birthing with pups born over a pupping season comparable to that of wild counterparts (Temte et al., 1991). This species demonstrated stronger latitudinal effect than that of any other North Pacific pinniped covered in this report, with an average shift of 4.1 days/°latitude. Whereas this relationship is similar to that previously described for wild Pacific harbor seals on the North American west coast south of 47°N, the larger captive data set allows better definition of a curvilinear relationship.

Temte et al. (1991) separated the Pacific harbor seal into three subgroups based on birth timing. The northernmost group, from northern British Columbia and Alaska has no latitudinal variation in birth timing. The late-birthing group inhabits Puget Sound, Washington, and pups two months later than coastal seals at the same latitudes. The southern group, as noted above, has highly significant latitudinal variation. Morphometric analysis of skulls from each of these populations supports the hypothesis of discrete populations (Temte, unpubl. data). No individuals from populations originating in Puget Sound, northern British Columbia or Alaska were included in this study.

The sex of the pup, maternal age, and the previous maternal cycle (pregnant vs. non-pregnant) had no effect on birth timing. These findings are from captive animals with dependable food supplies. In contrast, Boyd (1984) has suggested that maternal condition affects implantation timing in grey seals.

Latitudinal variation and photoperiod

For captive California sea lions, a smooth and continual temporal change of pupping dates across latitude occurred despite wide diversity of climatic conditions. Nevertheless, as almost all the captives could be traced to a single wild population on the California Channel Islands, a strong environmental component appears to influence birth timing. This pattern is highly suggestive of a response to a predictable, latitudinally dependent seasonal cue. The 6-month shift in birth timing between hemispheres, as demonstrated by California sea lions in New Zealand, strongly supports a photoperiod hypothesis. Furthermore, the decreasing variance to the north (in the Northern Hemisphere) is as expected if photoperiodism occurs (Bronson, 1985). At higher latitudes, organisms experience a greater rate of change in photoperiod. Consequently, responses to specific cues should occur over a compressed time period.

Latitudinal variation in birth timing of the northern fur seal, a species with delayed implantation (Daniel, 1981), can be explained by a response to photoperiod occurring between ovulation and implantation (Temte, 1985). This sets the time of implantation and birth while allowing flexibility in estrus timing. For example, arrival at breeding grounds and mating occur as much

as two months earlier for parous cows than for virgin northern fur seals (Craig, 1964; Bigg, 1986); this disparity is not reflected in birth timing (Trites, 1992). Gentry (1981) noted, however, that individual parous females have fairly rigid year-to-year estrus timing, and Bigg (1984) has suggested that the breeding synchrony found in this species may be due to arrival on shore and on social factors.

The harbor seal has been shown to have delayed implantation (Fisher, 1954; Bigg, 1969b) and the California and northern sea lions are thought to have this reproductive pattern as well (Odell, 1975; Boshier, 1981; Schusterman, 1981). Hence, a similar mechanism may exist to signal implantation in these species. Temte (1985) proposed that northern fur seals responded to a photoperiod of 12.5 hours per day (prior to the autumnal equinox), thus explaining the positive slope in latitudinal variation. Likewise, the Pacific harbor seals in this study have a positive slope and may respond to long (>12.0 h/day) photoperiods. In contrast, California sea lions have a negative slope in latitudinal variation, which suggests a response to a photoperiod slightly less than 12.0 hours per day (following the autumnal equinox), and occurring prior to implantation.

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Variations on a simple dynamic pool model

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Abstract.—A simple dynamic pool model (the "base model"), defined by a linear weight-at-age relationship and a Cushing (convex power) stock-recruitment relationship, results in an explicit solution for the fishing mortality rate corresponding to maximum sustainable yield F_{MSY}. This solution's sensitivity can be examined by comparing it to solutions derived under alternative model specifications. Four such modifications are considered here: 1) replacing the Cushing stock-recruitment equation with an equation of the Beverton-Holt form; 2) generalizing from linear growth to a flexible form of von Bertalanffy growth; 3) allowing the ages of recruitment to the fishery a_f and the mature stock a_m to diverge; and 4) allowing for a finite maximum age in the stock. Exact polynomial solutions for F_{MSY} are derived for each specification (except the fourth), and the potential bias introduced by use of the base model is examined for each. In all cases, the solution to the base model is within 10% of the solution to the alternative model under a range of parameter values.

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Some fishery models can be solved analytically (i.e., by mathematical manipulation of the equations), while others can be solved only numerically (i.e., by the brute force of computer simulation). One advantage of analytic models is that the generality of their solutions is more straightforwardly addressed. For example, it is easy to show that the stock size associated with maximum sustainable yield (MSY) in a Schaefer (1954) model is always one-half the pristine stock size; this property follows directly from the assumption of logistic growth upon which the model is based. Such generality is more difficult to demonstrate for simulation models, however. For instance, if a particular simulation showed that MSY was obtained at a stock size equal to one-half the pristine level, there would be no way to tell whether this result was general, except by repeated trial and error with different values for the input parameters.

Another example of an analytic solution is the one obtained by Thompson (1992) for the fishing mortality rate at MSY (F_{MSY}) in his simple dynamic pool model. Because this solution is an analytic one, it is completely general in the sense that it will hold whenever the underlying assumptions of the model hold, regardless of parameter values. Of course, the underlying assumptions may *not* hold in a particular instance, which raises the question: How sensitive is the solution to those assumptions? The purpose of this paper is thus to examine the sensitivity of Thompson's (1992) solution relative to the underlying assumptions of that model. This will be accomplished by developing four reasonable modifications to the base model proposed by Thompson and by examining the range of errors that might likely be encountered if the base model were employed in situations where one of the modifications would have been more appropriate.

Review of the base model

Thompson (1992, see also Jensen, 1973) defined a simple dynamic pool model as one that reflects the following assumptions: 1) cohort dynamics are of continuous-time form; 2) vital rates are constant with respect to time and age; 3) fish mature and recruit to the fishery continuously and at the same invariant ("knife-edge") age; 4) mean body weight at age is determined by age alone; 5) the stock (or population) consists of the pool of recruited individuals; 6) maximum age is infinite; 7) the stock is in an equilibrium state determined by the fishing mortality rate; and 8) recruitment is determined by stock biomass alone. Within the framework provided by these assumptions, particular models are distinguished by the forms assigned to the weight-at-age and stock-recruitment functions.

As an example, Thompson (1992) developed a particular simple dynamic pool model than can be solved explicitly for F_{MSY}. In terms of biomass per recruit, the model is basically

the same as that of Hulme et al. (1947), where body weight is assumed to be a linear function of age (e.g., Richards, 1969):

$$w(a) = w_r\left(\frac{a-a_r}{a_r-a_0}\right), \quad (1)$$

where a represents age, a_r is the age of recruitment, a_0 is the age intercept, $w(a)$ represents individual weight at age, and w_r is the weight at recruitment.

For a given recruitment level, stock biomass in the model is given by

$$B(F') = \left(\frac{b(F',a_r)}{M}\right)\left(\frac{1+K''+F'}{(1+F')^2}\right), \quad (2)$$

where M is the instantaneous rate of natural mortality, $F'=F/M$, $B(F')$ is the equilibrium stock biomass obtained under a relative fishing mortality rate of F', $b(F',a_r)$ is the equilibrium biomass at $a=a_r$ obtained under a relative fishing mortality rate of F', and

$$K'' = \frac{1}{M(a_r-a_0)}, \quad (3)$$

which can be interpreted in this model as the pristine ratio of growth to recruitment (Thompson, 1992).

Thompson (1992) extended the model described in Equation 2 by incorporating a stock-recruitment relationship of the convex power form suggested by Cushing (1971):

$$b(F',a_r) = pB(F')^q, \quad (4)$$

where p and q are constants and $0 \le q \le 1$. In the limiting case of $q=0$, recruitment is constant, while in the other limiting case of $q=1$, recruitment is proportional to biomass.

Substituting Equation 4 into Equation 2 and rearranging terms gives the following equation for equilibrium stock biomass:

$$B(F') = \left[\left(\frac{p}{M}\right)\left(\frac{1+K''+F'}{(1+F')^2}\right)\right]^{\frac{1}{1-q}}. \quad (5)$$

Multiplying both sides of Equation 5 by MF' then gives the equation for sustainable yield, which is maximized at

$$F'_{MSY} = \frac{-(q+1)K''+1+\sqrt{(q+1)^2K''^2+(6q-2)K''+1}}{2q} - 1, \quad (6)$$

where $F'_{MSY} = F_{MSY}/M$.

In the special case where $q=0$, Equation 6 reduces to the solution for F'_{max} ($=F_{max}/M$):

$$F'_{max} = \frac{K''+1}{K''-1}. \quad (7)$$

A common rule of thumb is that F'_{MSY} should equal 1 (Alverson and Pereyra, 1969; Thompson, 1992). The locus of parameter values for which this rule holds precisely is given by

$$q = \frac{1}{K''+2}. \quad (8)$$

Another behavior of interest is the ratio of $B(F'_{MSY})$ to $B(0)$. Here, this ratio has a lower limit of $(K''-1)/(4K'')$ (at $q=0$) and an upper limit of $1/e$ (at $q=1$).

The base model presented in Equations 1–6 can be modified in a number of ways. Although such modifications may make it more difficult to obtain an explicit solution for F_{MSY}, they may also provide some guidance as to the generality of the base model's behavior. Four modifications will be considered here: 1) replacing the Cushing stock-recruitment equation with an equation of the form suggested by Beverton and Holt (1957); 2) generalizing from linear growth to a flexible form of von Bertalanffy (1938) growth; 3) allowing the ages of recruitment to the fishery a_f and the mature stock a_m to diverge; and 4) allowing for a finite maximum age in the stock. For each modification (except the fourth), polynomial solutions for F'_{MSY}, F'_{max}, and the locus at which $F'_{MSY} = 1$ will be derived, and the upper limit to the ratio $B(F'_{MSY})/B(0)$ will be presented. The potential bias introduced by use of the base model will also be examined graphically for each modification.

Beverton-Holt recruitment

The choice of stock-recruitment relationship can have an appreciable impact on the resulting estimate of F_{MSY} (Kimura, 1988). For comparative purposes, the stock-recruitment relationship of Beverton and Holt (1957) can be substituted for the Cushing form used in the base model. It will prove convenient to parametrize the Beverton-Holt equation as follows:

$$b(F',a_r) = \frac{QB(F')}{PB(F')+1}, \quad (9)$$

where Q represents the slope of the curve at the origin and P represents the ratio between the slope at the origin and the height of the asymptote.

Substituting Equation 9 into Equation 2 and solving for $B(F')$ gives

$$B(F') = \left(\frac{1}{P}\right)\left(\frac{Q(1+K''+F')}{M(1+F')^2} - 1\right), \quad (10)$$

which is the analogue to Equation 5 for the Beverton-Holt recruitment case.

Polynomial solution

Multiplying Equation 10 through by MF', differentiating with respect to F', and setting the resulting expression equal to zero gives the following polynomial solution for F'_{MSY}:

$$F'^{3}_{MSY}+3F'^{2}_{MSY}+[3+(K''-1)Q']F'_{MSY}+1-(K''+1)Q'=0, \quad (11)$$

where $Q' = Q/M$.

It is possible to solve Equation 11 explicitly for F'_{MSY}. For the case where $K''>1$,

$$F'_{MSY} = \left[Q'\left(\sqrt{K''^{2} + Q'\left(\frac{K''-1}{3}\right)^{3}} + K''\right)\right]^{1/3} - \left[Q'\left(\sqrt{K''^{2} + Q'\left(\frac{K''-1}{3}\right)^{3}} - K''\right)\right]^{1/3} - 1. \quad (12)$$

For the case where $K''=1$,

$$F'_{MSY} = (2Q')^{1/3} - 1. \quad (13)$$

For the case where $K''<1$,

$$F'_{MSY} = 2\sqrt{\frac{1-K''}{3}Q'}\cos\left(\left(\frac{1}{3}\right)\cos^{-1}\left[\left(\frac{3K''}{1-K''}\right)\sqrt{\frac{3}{(1-K'')Q'}}\right]\right) - 1 . \quad (14)$$

The parameter Q' functions inversely to q in the sense that Equations 11–14 reduce to Equation 7 as Q' approaches infinity (the F'_{max} case), whereas Equation 6 does so as q approaches zero. As Q' increases, F'_{MSY} increases monotonically, whereas F'_{MSY} decreases with increasing q in the base model.

As with the base model, Equations 11–14 contain $F'_{MSY} = 1$ as a special case. Here this is obtained when $Q' = 4$ or when K'' approaches infinity. This contrasts somewhat with the base model, where keeping F'_{MSY} at a constant value of 1.0 required an inverse relationship between q and K''. However, it should be pointed out that $F'_{MSY} = 1$ is a very special case in the Beverton-Holt form of the model, since this turns out to be the only constant value of F'_{MSY} that does not imply some sort of relationship between Q' and K''. In fact, a direct relationship between Q' and K'' is required for all constant values of $F'_{MSY} > 1$, as described below:

$$Q' = \frac{(F'_{MSY}+1)^{3}}{F'_{MSY}+1-(F'_{MSY}-1)K''} . \quad (15)$$

Another difference between this model and the base model is that here F'_{MSY} reaches zero at $Q'=1/(K''+1)$, whereas F'_{MSY} in the base model does not reach zero until $q=1$. Still another difference is that here the upper limit to the ratio $B(F'_{MSY})/B(0)$ is 0.5, contrasted with $1/e$ in the base model. In both models, this limit is reached as F'_{MSY} approaches zero.

Finally, the behavior of this modification differs from that of the base model in that extinction is possible here, owing to the Beverton-Holt curve's finite slope at the origin. Extinction occurs here at

$$F'_{ext} = \frac{Q' + \sqrt{(4K''+Q')Q'}}{2} - 1. \quad (16)$$

The relative fishing mortality rate described by Equation 16 need not be unrealistically high. For example, it will be less than F'_{max} whenever the following relationship holds:

$$Q' < \frac{4K''}{K''^{2}-1} . \quad (17)$$

Bias resulting from the assumption of Cushing recruitment

Assuming that the stock-recruitment relationship follows the Cushing form when it actually follows a Beverton-Holt form can lead to a biased estimate of F_{MSY}. To compare stock-recruitment curves, Kimura (1988) observed that a two-parameter function can be defined by any two points on the curve. In his example, Kimura used hypothetical stock-recruitment "observations" at the pristine biomass level and at one-half the pristine biomass level. Kimura conjectured that recruitment might be reduced to about 90% of the pristine level when biomass has been reduced by 50% relative to its own pristine level, a suggestion which has been endorsed by others (e.g., Clark, 1991). Given the other parameters used in his example, Kimura found that the F_{MSY} value under a Beverton-Holt stock-recruitment relationship was much less than the value under a Cushing relationship fit to the same two stock-recruitment points.

However, there is no reason to believe *a priori* that a Cushing relationship is necessarily less conservative than a Beverton-Holt relationship in terms of its associated F_{MSY} value. Note that Equation 6 can be solved explicitly for q as a function of K'' and F'_{MSY} as follows:

$$q = \frac{K''+1-(K''-1)F'_{MSY}}{(K''+1+F'_{MSY})(F'_{MSY}+1)} . \quad (18)$$

Substituting Equation 12, 13, or 14 into Equation 18 thus gives the q value that sets F_{MSY} under a Cushing stock-recruitment relationship equal to F_{MSY} under a Beverton-Holt relationship. Assuming that both stock-recruitment curves are parametrized to pass through the same pristine stock-recruitment point $(B(0),b(0,a_r))$, this q value implies a second intersection at some lower biomass level. It turns out that this lower level is always less than about 20% of $B(0)$ (Fig. 1A) and greater than about 20% of $b(0,a_r)$ (Fig. 1B). In other words, Kimura's (1988) placement of a lower intersection at 50% of $B(0)$ would always cause the Cushing model to overestimate F_{MSY}. Placing the lower intersection at a biomass level less than 20% of $B(0)$, however, might result in either an over- or underestimate.

For example, one rule of thumb (Clark, 1991) holds that $F_{0.1}$ (the fishing mortality rate that reduces the slope of the yield-per-recruit curve to one-tenth of the slope at the origin), $F_{35\%}$ (the fishing mortality rate that reduces the level of spawning biomass per recruit to 35% of the pristine level) and M should be approximately equal. In the base model, this rule of thumb holds exactly at K''=1.5 (Thompson, in press). In the base model with Beverton-Holt recruitment, then, F_{MSY}=$F_{0.1}$=$F_{35\%}$=M at Q'=4 and K''=1.5. These parameters imply a stock-recruitment curve in which recruitment is reduced from $b(0,a_r)$ by exactly 1/11 when biomass is reduced to 50% of $B(0)$, and in which recruitment is reduced from $b(0,a_r)$ by exactly 50% when biomass is reduced to 1/11 of $B(0)$.

In the base model with Cushing recruitment, on the other hand, F_{MSY}=$F_{0.1}$=$F_{35\%}$=M at q=2/7 and K''=1.5, implying a stock-recruitment curve in which recruitment is reduced from $b(0,a_r)$ by about 18% when biomass is reduced to 50% of $B(0)$, and in which recruitment is reduced from $b(0,a_r)$ by about 50% when biomass is reduced to 1/11 of $B(0)$. Thus, in the "rule of thumb" case, the form of the stock-recruitment curve (Cushing or Beverton-Holt) has virtually no impact on the resulting estimate of F_{MSY} so long as the curve passes through $(B(0),b(0,a_r))$ and $(B(0)/11,b(0,a_r)/2)$.

More generally, to cause Cushing and Beverton-Holt curves to intersect at $(B(0),b(0,a_r))$ and at some fraction ρ of $B(0)$, set

$$q = 1 - \frac{\ln(\rho[(K''+1)(Q'-1)]+1) - \ln(Q') - \ln(K''+1)}{\ln(\rho)} \quad (19)$$

and

$$p = \left(\frac{M}{K''+1}\right)\left(\frac{(K''+1)(Q'-1)}{P}\right)^{1-q}. \quad (20)$$

Alternatively, the lower intersection can also be defined in terms of relative recruitment (as opposed to relative biomass). To cause Cushing and Beverton-Holt curves to intersect at $(B(0),b(0,a_r))$ and at some fraction θ of $b(0,a_r)$, set

$$q = 1 - \frac{\ln(\theta)}{\ln(\theta) - \ln[(1-\theta)(K''+1)Q'+\theta]} \quad (21)$$

and p as in Equation 20.

Biases resulting from placement of the lower intersection at 50% and 10% of $B(0)$ are compared in Figure 2, A and B, respectively. Note that use of the 50% value (as in Kimura's [1988] example) causes large and uniformly positive biases in the base model's estimate of F_{MSY}. On the other hand, use of the 10% value constrains bias to the +/– 10% range over a large portion of parameter space.

Biases resulting from placement of the lower intersection at 90% and 50% of $b(0,a_r)$ are compared in Figure 2, C and D, respectively (the 50% reference point has been suggested by Mace[1] and Myers et al.[2]). As with the relative biomass reference level, use of Kimura's (1988) relative recruitment reference level (90%) causes large and uniformly positive biases in the base model's estimate of F_{MSY} over a large portion of parameter space. On the other hand, use of the 50% value constrains bias to the +/– 10% range over a sizable region.

As Figure 2 illustrates, then, there is reason to believe that the form of the stock-recruitment curve (Cushing or Beverton-Holt) may not be particularly important in terms of the resulting estimate of F_{MSY} so long as the candidate curves intersect at a fairly low level. In other words, fishery managers need not always view an estimate of F_{MSY} as being critically dependent on the form of the stock-recruitment curve.

A general growth function

The linear growth function used by Thompson (1992) may be viewed as a special case of the following more

[1]Mace, P. M. 1993. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., 1335 East-West Highway, Silver Spring, MD 20910.

[2]Myers, R. A., A. A. Rosenberg, P. Mace, N. Barrowman, and V. Restrepo. 1993. In search of thresholds for recruitment overfishing. Dep. Fisheries and Oceans, St. John's, New Foundland. Unpubl. manuscr., 14 p.

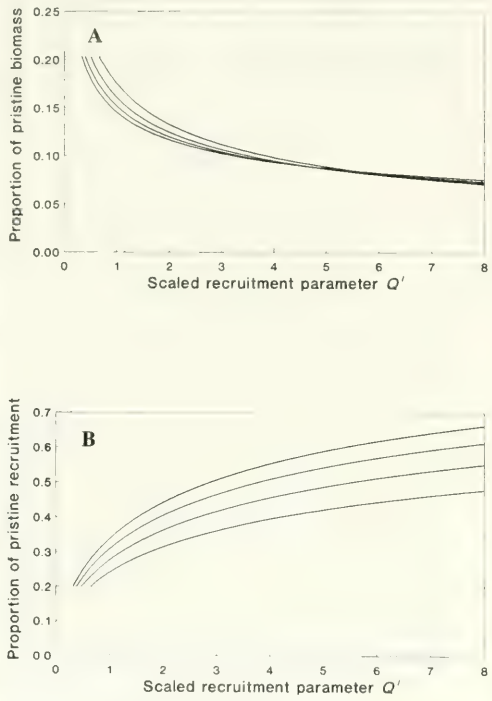

Figure 1

Location of the zero-bias intersection of the Cushing and Beverton-Holt stock-recruitment curves. Horizontal dashed lines represent limiting values, obtained in the limit as F_{MSY} goes to zero. Proceeding from left to right along a given horizontal dashed line, the curves which intersect the line correspond to K'' values of 2.0, 1.5, 1.0, and 0.5, respectively. Given values of the composite parameter K'' and the scaled Beverton-Holt recruitment parameter Q', fixing the lower intersection of the recruitment curves at the point identified by the appropriate locus in this figure causes the base model to give the same value for F'_{MSY} as the Beverton-Holt modification. (**A**) Zero-bias intersection defined in terms of relative stock biomass. Points below and to the left of the curves result in negative bias, while points above and to the right of the curves result in positive bias. (**B**) Zero-bias intersection defined in terms of relative recruitment. Points below and to the right of the curves result in negative bias, while points above and to the left of the curves result in positive bias.

general form:

$$w(a) = w_r \left(\frac{1 - e^{K''(a - a_0)/(K''+1)}}{1 - e^{K''(a_r - a_0)/(K''+1)}} \right)^n, \qquad (22)$$

where K is Brody's growth coefficient, $K' = K/M$, and n is a positive integer. In different parametrizations, Equation 22 corresponds to (or is a special case of) a number of general growth functions, including those of Richards (1959, see also Fletcher, 1975), Savageau (1980), and Schnute (1981). Schnute described his parametrization of Equation 22 as "generalized von Bertalanffy growth" (although he did not restrict n to integer values). When n=3, Equation 22 corresponds to the common ("specialized") von Bertalanffy (1938) curve, and, when n=1, the "monomolecular" curve of Pütter (1920) and Brody (1928) is obtained.

In the limit as K approaches zero, Equation 22 gives an nth-degree polynomial in age:

$$w(a) = w_r \left(\frac{a - a_0}{a_r - a_0} \right)^n, \qquad (23)$$

which has been used to describe growth (though not always in weight) by Mendelsohn (1963), Dethlefsen et al. (1968), Knight (1968), Rafail (1972), Roff (1980), Geoghegan and Chittenden (1982), Standard and Chittenden (1984), and Chen et al. (1992). Equation 1 thus represents the special case of Equation 22 where K approaches zero and n=1.

Polynomial solution

The polynomial solution for this model is partitioned into two cases (K=0 and K>0) and derived in the Appendix.

When K=0, the solution for F'_{max} can be written as a polynomial of degree n, and the solution for F'_{MSY} can be written as a polynomial of degree n+1. When K>0, the solution for F'_{max} can be written as a polynomial of degree $2n$, and the solution for F'_{MSY} can be written as a polynomial of degree $2n$+1. As with the base model, the solution in either case indicates that maintaining an F'_{MSY} value of 1.0 requires an inverse relationship between q and K'' (which, as in the base model, can be written explicitly). Likewise, the upper limit to the ratio $B(F'_{MSY})/B(0)$ is the same as in the base model ($1/e$) in both cases.

The polynomial solution can be manipulated easily to show how it varies across the range of possible K', q, and K'' values. For example, several limiting values of F'_{max} and F'_{MSY} are shown in Table 1.

Bias resulting from the assumption of linear growth

Assuming that growth is linear when it actually follows a generalized von Bertalanffy form can lead to a

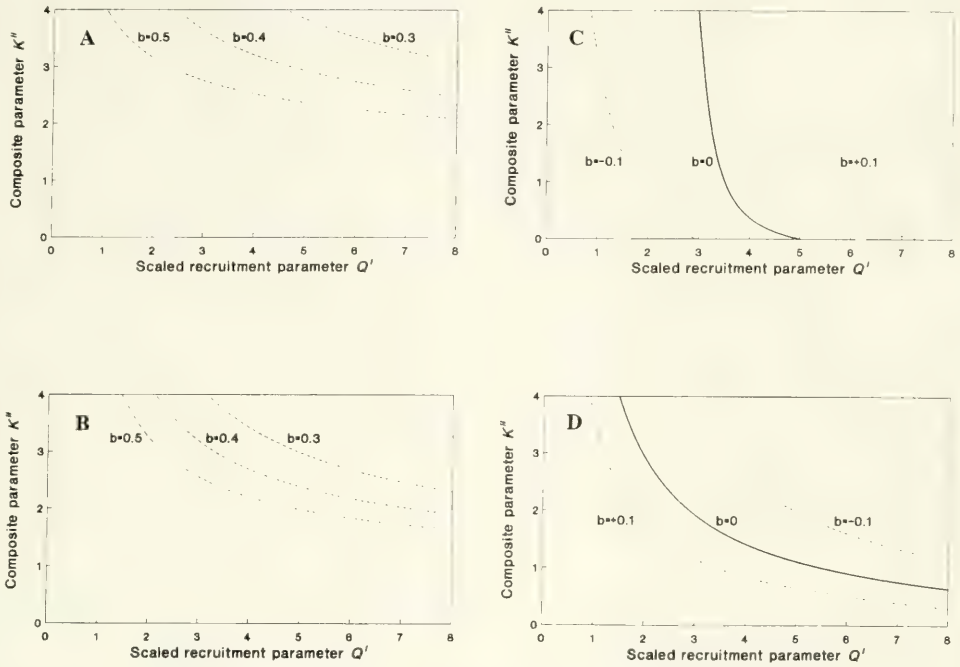

Figure 2

Isobias loci obtained when the base model is used to approximate the Beverton-Holt modification under four calibration methods. (**A**) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 50% of pristine biomass. Loci corresponding to biases in F'_{MSY} of 30% (b=0.3), 40% (b=0.4), and 50% (b=0.5) are shown. (**B**) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 10% of pristine biomass. Loci corresponding to biases in F'_{MSY} of −10% (b=−0.1), 0% (b=0), and +10% (b=+0.1) are shown. (**C**) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 90% of pristine recruitment. Loci corresponding to biases in F'_{MSY} of 30% (b=0.3), 40% (b=0.4), and 50% (b=0.5) are shown. (**D**) Isobias loci obtained when the lower intersection of the Cushing and Beverton-Holt stock-recruitment curves is fixed at 50% of pristine recruitment. Loci corresponding to biases in F'_{MSY} of +10% (b=+0.1), 0% (b=0), and −10% (b=−0.1) are shown.

biased estimate of F_{MSY}. One way to compare the two types of curve is to require that they intersect at w_r and that they imply the same pristine biomass-per-recruit level. In the base model, stock biomass per recruit is obtained by multiplying Equation 2 through by $w_r/b(F',a_r)$. When Equation 22 or 23 is used to represent growth, stock biomass per recruit is given by Appendix Equation 5 or Appendix Equation 11. When growth curves are forced to intersect at w_r and pristine biomass per recruit levels are equated, the following parametrization is defined:

$$\hat{K}'' = (1 - e^{-K''K'})^{n} \left(\sum_{k=0}^{n} \frac{(-1)^k \binom{n}{k} e^{-kK''K'}}{kK' + 1} \right) - 1, \qquad (24)$$

where $\binom{n}{k}$ is the binomial coefficient (Appendix) and $\hat{K}''$ is the estimated value of K'' used to define the linear growth relationship (assuming that M and a_r are the same under both weight-at-age relationships, $\hat{K}''$ is distinguished from K'' by the fact that the age intercepts of the two curves differ—Equation 3).

Substituting Equation 24 for $\hat{K}''$ in Equation 6 gives F'_{MSY} in the base model when the linear growth function is fit in the manner described above. This F'_{MSY} value can be either higher or lower than the value given by the solution derived in the Appendix. For the case where n=3, Figure 3 shows the range of +/− 10% bias for four values of K'', along with the loci of zero bias. Note that at low values of K'' (e.g., 0.5), the two

Table 1
Limits on F'_{max} and F'_{MSY} under generalized von Bertalanffy growth.

	$K' = 0$	$K' \to \infty$
Limits on F'_{max}		
$K'' \to \infty$	$F'_{max} = \frac{1}{n}$	$F'_{max} \to \infty$
$F'_{max} \to \infty$	$K'' = \lim_{h \to 0} \left(\frac{K'}{\ln(nK' + 1)} \right) = \frac{1}{n}$	$K'' \to \infty$
Limits on F'_{MSY}		
$K'' \to \infty$	$F'_{MSY} = \frac{1-q}{n+q}$	$F'_{MSY} = \frac{1-q}{q}$
$K'' = 0$	$F'_{MSY} = \frac{1-q}{q}$	$F'_{MSY} = \frac{1-q}{q}$

F'_{MSY} values tend to be close over a large portion of parameter space, but that as K'' increases, the base model's estimate of F'_{MSY} is more likely to be significantly biased.

Divergent ages of recruitment and maturity

As defined by Thompson (1992), all simple dynamic pool models assume that fish recruit to both the fishery and the mature stock at a single age a_r. However, in more complicated dynamic pool models, it is common for the age (or size) of recruitment to the fishery to be treated as a management variable.

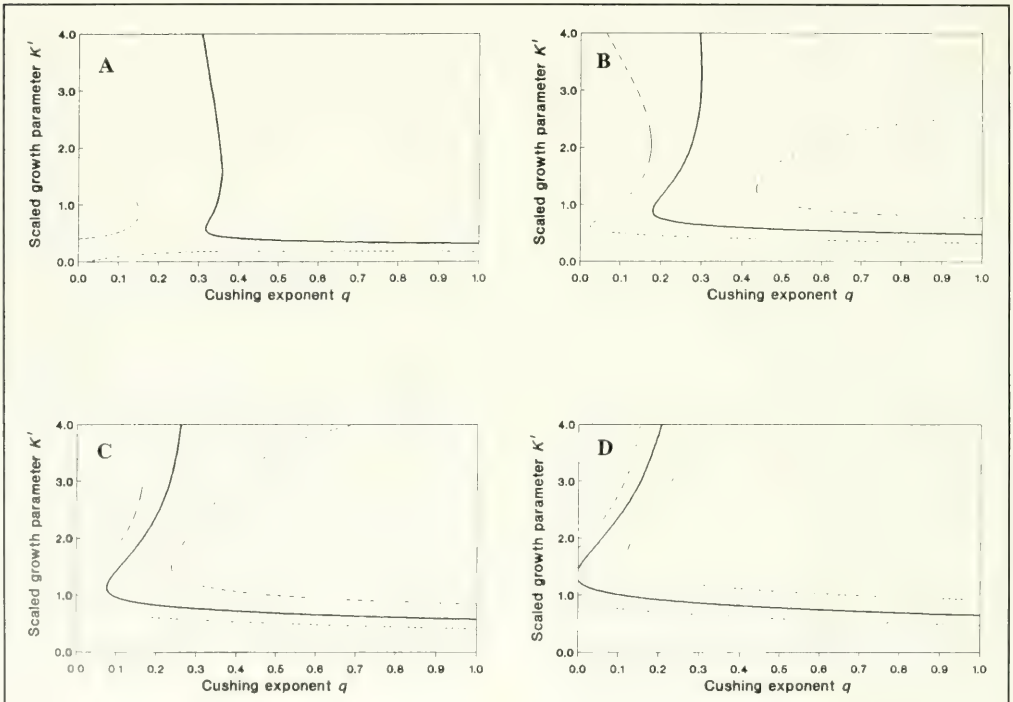

Figure 3
Isobias loci obtained when the base model is used to approximate the generalized von Bertalanffy modification under four values of the composite parameter K (n=3 in all cases). Solid curves indicate loci of zero bias in F'_{MSY}. The dashed curve to the left of the solid curve in each panel indicates the locus of +10% bias, while the dashed curve on the right indicates the locus of −10% bias. (**A**) Isobias loci for K''=0.5. (**B**) Isobias loci for K''=1.0. (**C**) Isobias loci for K''=1.5. (**D**) Isobias loci for K''=2.0.

To accommodate this change, the Cushing stock-recruitment relationship (Equation 4) has to be rewritten to specify that only the mature biomass $B_m(F')$ contributes to recruitment:

$$b(F',a_f) = p\,B_m(F')^q. \tag{25}$$

Equation 2 can be rewritten to express total fishable biomass as

$$B_f(F') + \left(\frac{b(F',a_f)}{M}\right)\left(\frac{1 + K_f'' + F'}{(1+F')^2}\right), \tag{26}$$

where $K_f'' = 1/[M(a_f - a_0)]$, after Equation 3.

Polynomial solution

Age at recruitment exceeds age at maturity In the case where a_f exceeds a_m, recruitment to the fishery and to the mature stock are related as follows:

$$b(F',a_f) = b(F',a_m)\left(\frac{w(a_f)}{w(a_m)}\right) e^{M(a_f - a_m)} = b(F',a_m)\left(\frac{K_m''}{K_f''}\right) e^{\left(\frac{1}{K} - \frac{1}{K}\right)}, \tag{27}$$

where $K_m'' = 1/[M(a_m - a_0)]$, after Equation 3.

Total mature biomass can then be expressed as

$$\begin{aligned} B_m(F') &= \left(\frac{b(F',a_m)}{a_m - a_0}\right)\int_{a_0}^{a_m}(a - a_0)e^{M(a-a_0)}da + B_f(F') \\ &= \left(\frac{b(F',a_m)}{M}\right)\left[\left(1 + \frac{1}{M(a_m - a_0)}\right)\right. \\ &\quad \left. - e^{M(a_m - a_0)}\left(\frac{a_f - a_0}{a_m - a_0} + \frac{1}{M(a_m - a_0)}\right)\right] + B_f(F') \\ &= \left(\frac{b(F',a_m)}{M}\right)\left[1 + K_m'' - e^{\left(\frac{1}{K} - \frac{1}{K}\right)}\left(\frac{K_m''}{K_f''} + K_m''\right)\right] + B_f(F') \\ &= \frac{b(F',a_m)\,(1 + K_m'') - b(F',a_f)\,(1 + K_f'')}{M} + B_f(F'). \end{aligned} \tag{28}$$

Equations 25–28 constitute a set of four equations in four unknowns [$b(F',a_f)$, $b(F',a_m)$, $B_f(F')$, and $B_m(F')$]. Solving simultaneously gives

$$B_f(F') = \left(\frac{p}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right)\left[\left(\frac{p}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right) + \alpha(K_f'')\right]^{\frac{q}{1-q}}, \tag{29}$$

where

$$\alpha(K_f'') = \left(\frac{K_f''}{K_m''}\right)\left(\frac{1 + K_m''}{e^{-\left(\frac{1}{K} - \frac{1}{K}\right)}}\right) - K_f'' - 1. \tag{30}$$

Multiplying Equation 29 through by MF', differentiating with respect to F', and setting the resulting expression equal to zero gives the following polynomial solution for F'_{MSY} (which collapses to Equation 6 when $K_f'' = K_m''$):

$$\begin{aligned} &\left((1-q)[\alpha(K_f'')(1-K_f'')+1]-1\right)F'^3_{MSY} + \\ &\left((1-q)[\alpha(K_f'')(3-K_f'')+2K_f''+3]-3K_f''-2\right)F'^2_{MSY} + \\ &(1-q)[\alpha(K_f'')(3+K_f'')+K_f''^2+4K_f''+3]-2K_f''^2-3K_f''-1)F'_{MSY} + \\ &(1-q)[\alpha(K_f'')(1+K_f'')+K_f''^2+2K_f''+1] = 0. \end{aligned} \tag{31}$$

The solution for F'_{max} in this model is the same as in the base model (Equation 7).

Equation 31 contains $F'_{MSY} = 1$ as a special case, obtained when the following relationship holds:

$$q = 1 - \frac{(K_f'' + 2)\,(K_f'' + 1)}{4\alpha(K_f'') + (K_f'' + 2)^2}. \tag{32}$$

Just as the base model required an inverse relationship between q and K'' in order for F'_{MSY} to equal 1.0 (Equation 8), this model requires an inverse relationship between q and K_f''. Likewise, the upper limit to the ratio $B(F_{MSY})/B(0)$ is the same as in the base model ($1/e$).

Age at maturity exceeds age at recruitment Another possible modification is to allow a_m to exceed a_f. This requires rewriting Equation 27 as follows:

$$b(F',a_f) = b(F',a_m)\left(\frac{K_m''}{K_f''}\right) e^{(1+F')\left(\frac{1}{K} - \frac{1}{K}\right)}. \tag{33}$$

The previous expressions for recruitment (Equation 25) and equilibrium fishable biomass (Equation 26) can be applied without modification. However, because the entire mature stock is subject to both fishing and natural mortality, the previous expression for equilibrium mature biomass (Equation 28) is simplified to

$$B_m(F') = \left(\frac{b(F',a_m)}{M}\right)\left(\frac{1 + K_m'' + F'}{(1+F')^2}\right). \tag{34}$$

Solving Equations 25, 26, 33, and 34 simultaneously gives

$$B_f(F') = \left(\frac{p}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right)\left[\left(\frac{p}{M}\right)\left(\frac{1+K_m''+F'}{(1+F')^2}\right)\times \left(\frac{K_f''}{K_m''}\right) e^{-(1+F')\left(\frac{1}{K}-\frac{1}{K}\right)}\right]^{\frac{q}{1-q}}. \quad (35)$$

The fact that F' appears in the exponent in Equation 35 complicates the solution for F'_{MSY} somewhat, increasing the degree of the polynomial solution to four:

$$\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)qF'^{4}_{MSY}+\left[(K_f''+K_m''+3)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)+1\right]qF'^{3}_{MSY}+\left[(K_f''K_m''+2K_f''+2K_m''+3)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)q+(2K_m''+3)q+K_f''-1\right]F'^{2}_{MSY}+\left[(K_f''+1)(K_m''+1)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)q+(K_f''+3)(K_m''+1)q+K_f''K_m''-K_m''-2\right]F'_{MSY}-(K_f''+1)(K_m''+1)(1-q)=0. \quad (36)$$

The solution for F'_{max} is the same as in the base model (Equation 7).

Equation 36 contains $F'_{MSY}=1$ as a special case, obtained when the following relationship holds:

$$q=\frac{K_m''+2}{(K_f''+2)(K_m''+2)\left(\frac{1}{K_m''}-\frac{1}{K_f''}\right)+K_f''(K_m''+1)+3K_m''+4}. \quad (37)$$

As with the base model (Equation 8), the above expression implies an inverse relationship between q and K_f'. Likewise, the upper limit to the ratio $B(F'_{MSY})/B(0)$ remains the same ($1/e$).

Bias resulting from the assumption of $a_f=a_m$

When $a_f>a_m$, Equation 6 tends to underestimate F'_{MSY}. Loci of –10% bias are shown in Figure 4A for four values of K_m''. Parameter combinations above a particular curve and below the horizontal line $K_f''=K_m''$ result in an F'_{MSY} estimate that is within 10% of the value given by Equation 31. Note that the base model's solution is fairly sensitive to K_f'' when K_m'' is low. For example, when $K_m''=0.5$, almost any value of $K_f''<K_m''$ will result in Equation 6 underestimating F'_{MSY} by more than 10%. At higher K_m'' values (e.g., $K_m''>1$), the base model's solution is less sensitive.

The results for the case where $a_f<a_m$ are similar, except that here Equation 6 tends to overestimate rather than underestimate F'_{MSY}. Loci of +10% bias are shown in Figure 4B for four values of K_m''. Parameter combinations below a particular curve and above the horizontal line $K_f''=K_m''$ result in an F'_{MSY} estimate that is within 10% of the value given by Equation 31. Again, the base model's solution is fairly sensitive to K_f'' when K_m'' is low (e.g., $K_m''=0.5$), while at higher values (e.g., $K_m''>1$), the base model's solution is less sensitive.

Finite maximum age

As defined by Thompson (1992), all simple dynamic pool models exhibit mortality and growth rates which are independent of age (above the age of recruitment). This implies that there is no maximum age. However, in more complicated dynamic pool models, it is common to specify a maximum age above which all remaining fish die in knife-edge fashion. As noted by Fletcher (1987), misspecification of maximum age can introduce significant bias into some models. When the base model is modified so as to exhibit a finite maximum age (a_{max}), Equation 5 will tend to overestimate true equilibrium stock biomass, which can be written as

$$B(F') = \left[\left(\frac{p}{M}\right)\left(\frac{K''+1+F'}{(1+F')^2}-\left(\frac{K''_{max}+1+F'}{(1+F')^2}\right)\left(\frac{K''}{K''_{max}}\right)e^{-(1+F')\left(\frac{1}{K}-\frac{1}{K}\right)}\right)\right]^{\frac{1}{1-q}}, \quad (38)$$

where $K''_{max}=1/[M(a_{max}-a_0)]$, after Equation 3. The difference inside the exterior parentheses in Equation 38 is proportional to the difference between two calculations of stock biomass per recruit in a population with infinite maximum age, where the first calculation begins the integral (over age) at age a_r and the second begins at age a_{max}. Subtracting the second term from the first adjusts for the assumption of a maximum age at $a=a_{max}$.

Because of the presence of F' in the exponential term in Equation 38, it is not possible to solve for F'_{MSY} explicitly in this modification.

Bias resulting from the assumption of infinite maximum age

Note that as K''_{max} becomes small (e.g., as a_{max} becomes large), the proportion surviving to the maximum age (the exponential term in Equation 38) goes to zero and

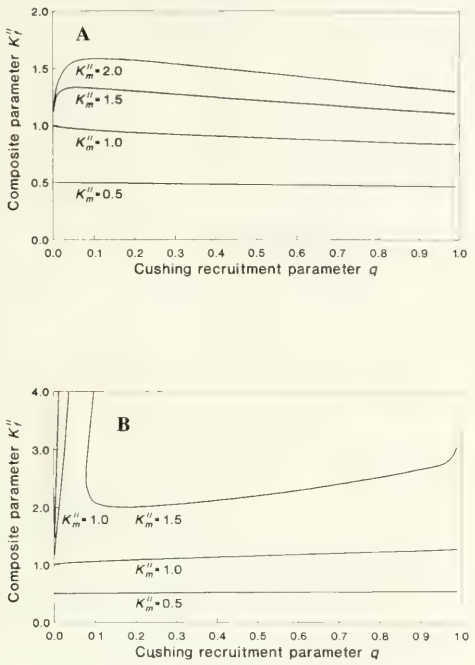

Figure 4

Isobias loci obtained when the base model is used to approximate the modification in which the ages of recruitment to the fishery and to the mature stock diverge. (**A**) Loci of –10% bias in F'_{MSY} obtained when the age of recruitment to the fishery is greater than the age of recruitment to the mature stock. (**B**) Loci of +10% bias in F'_{MSY} obtained when the age of recruitment to the fishery is less than the age of recruitment to the mature stock.

Equation 38 collapses to Equation 5. However, at any positive value of K''_{max}, Equation 5 will tend to overestimate the true value of $B(F')$ to some extent. Conversely, Equation 6 will tend to underestimate the true value of F'_{MSY}. Figure 5 shows loci of –10% bias in Equation 6's estimate of F'_{MSY}. Points above and to the left of the curves result in a bias of less than 10% (absolute value). For example, a stock with M=0.2, a_0=–1, and a_{max}=24 would have a K''_{max} value of 0.2. For such a stock, Equation 6's estimate of F'_{MSY} would be within 10% of the correct value for any value of K''>0.5 so long as q was less than about 0.53.

Conclusion

Four modifications to the base model presented by Thompson (1992) have been considered (Beverton-Holt recruitment, generalized von Bertalanffy growth, divergent ages of recruitment and maturity, and finite maximum age). The first three modifications all increase the degree of the polynomial solution for F_{MSY} (Table 2), while the fourth modification renders a polynomial solution impossible.

In order to make the Cushing stock-recruitment form of the model comparable to the Beverton-Holt form, an acceptable approximation can often be made by equating the pristine stock-recruitment points and placing the other (nonzero) intersection of the stock-recruitment curves at a fairly low level (e.g., at 10% of the pristine biomass level or at 50% of the pristine recruitment level).

In order to make the linear growth form of the model comparable to the generalized von Bertalanffy growth form, an acceptable approximation can often be made by equating the weights at recruitment and the pristine biomass-per-recruit ratios.

When the ages of recruitment to the fishery and to the mature stock diverge sufficiently or when the maximum age in the stock is sufficiently low, the base model can produce a significantly biased estimate of F_{MSY}. Except for the case in which the age of recruitment to the fishery precedes the age of recruitment to the mature stock, though, it is helpful to note that the base model always errs on the conservative side.

In conclusion, it appears that simple models (at least the base model considered here) may often perform adequately even when the true dynamics of the system follow more complicated formulae. This tends to confirm the results of studies by Silliman (1971), Roff (1983), and Ludwig and Walters (1985), who also found that simple models could perform at least as well as more complex versions in a variety of situations.

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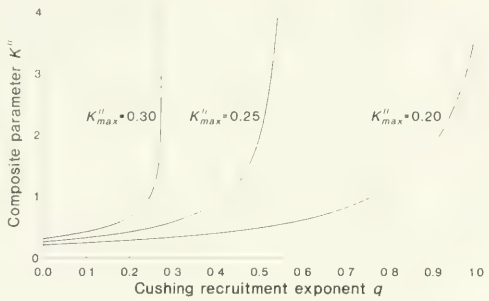

Figure 5

Loci of −10% bias in F'_{MSY} obtained when the base model is used to approximate the modification in which the maximum age in the population is finite. Points above and to the left of the curves correspond to a bias of less than 10% (absolute value), while points below and to the right of the curves correspond to a bias of greater than 10% (absolute value).

Table 2

Degree of polynomial solutions for F'_{MSY} under various modifications.

Modification	Degree
Beverton-Holt stock-recruitment	3
Generalized von Bertalanffy growth	
K=0	n+1
K>0	2n+1
Divergent ages of recruitment and maturity	
$a_r > a_m$	3
$a_r < a_m$	4

helpful. Several anonymous reviewers also supplied constructive suggestions.

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Appendix

Some combinatoric terms

In order to incorporate Equations 22 or 23 into the model, it is helpful to define a few concepts taken from combinatorial theory (the notation used here follows Riordan [1980]). First, the number of permutations of n objects taken k at a time is given by

$$(n)_k = \frac{n!}{(n-k)!}, \tag{A1}$$

with $(n)_k$ defined as zero for $k<0$ or $k>n$.

The number of combinations (i.e., permutations without regard to order) of n objects taken k at a time is given by the binomial coefficient

$$\binom{n}{k} = \frac{(n)_k}{k!} = \frac{n!}{k!\,(n-k)!}, \tag{A2}$$

with $\binom{n}{k}$ defined as zero for $k<0$ or $k>n$.

The number of ways in which an n-element set can be partitioned into k subsets is given by Stirling numbers of the second kind, written

$$S(n,k) = \left(\frac{1}{k!}\right)\sum_{\lambda=0}^{k}(-1)^{k-\lambda}\binom{k}{\lambda}\lambda^n. \tag{A3}$$

The coefficients of the polynomial expansion of $(x)_n$ are given by Stirling numbers of the first kind, written

$$s(n,k) = \sum_{\lambda=0}^{n-k}(-1)^{\lambda}\binom{n-1+\lambda}{n-k+\lambda}\binom{2n-k}{n-k-\lambda}S(n-k+\lambda,\lambda). \tag{A4}$$

Polynomial solution for a generalized growth function

***K*=0** Beginning with the simpler case where $K=0$ (Equation 23), stock biomass per recruit can be written

$$\begin{aligned} BPR(F') &= \int_a^{\cdot} w_r\left(\frac{a-a_r}{a_r-a_0}\right)^n e^{-M(1+F)(a-a_r)}\,da \\ &= \left(\frac{w_r}{M}\right)\sum_{k=0}^{n}\frac{(n)_k K^{n-k}}{(1+F')^{k+1}}. \end{aligned} \tag{A5}$$

In general, stock biomass in any simple dynamic pool model with Cushing recruitment can be written as the following function of biomass per recruit:

$$B(F') = \left(\frac{pBPR(F')}{w_r}\right)^{\frac{1}{1-q}}. \tag{A6}$$

Substituting Appendix Equation 5 (A5) into Appendix Equation 6 (A6), multiplying through by MF', and differentiating gives the following expression:

$$\begin{aligned} \frac{dY(F')}{dF'} = \left(\frac{pB(F')^q}{(1-q)(1+F')^{n+2}}\right) \cdot \\ \left(\sum_{k=0}^{n}[(n)_k K^{n-k}(1-kF')(1+F')^{n-k}] - \right. \\ \left. q\sum_{k=0}^{n}[(n)_k K^{n-k}(1+F')^{n-k+1}]\right). \end{aligned} \tag{A7}$$

The solution to Equation A7 can be written as a polynomial of degree $n+1$ as follows:

$$\sum_{i=0}^{n}\left(\sum_{k=0}^{n}\left[\binom{n-k}{i}-k\binom{n-k}{i-1}\right](n)_k K'^k - \left[\sum_{k=0}^{n}\binom{n+1-k}{i}(n)_k K'^k\right]q\right)F'^{\,i}_{MSY} - qF'^{\,n+1}_{MSY} = 0. \quad \text{(A8)}$$

In the special case where q=0, Equation A8 gives the following polynomial solution for F'_{max}:

$$\sum_{i=0}^{n}\left(\sum_{k=0}^{n}\left[\binom{n-k}{i}-k\binom{n-k}{i-1}\right](n)_k K'^k\right)F'^{\,i}_{max}=0. \quad \text{(A9)}$$

Equation A7 can be solved explicitly for q. The locus at which F'_{MSY}=1 is given by

$$q=\left(\frac{1}{2}\right)\left(1-\frac{\sum_{k=0}^{n}\left[k(n)_k\left(\frac{K'}{2}\right)^k\right]}{\sum_{k=0}^{n}\left[(n)_k\left(\frac{K'}{2}\right)^k\right]}\right). \quad \text{(A10)}$$

Note that Equations 6–8 constitute the special cases of Equations A8–A10 where n=1.

***K*>0** When growth follows the form of Equation 22, stock biomass per recruit can be written

$$BPR(F')=\int_{a_r}^{\infty} w_r\left(\frac{1-e^{-K(a-a_r)-K'K}}{1-e^{K'K}}\right)^n e^{M(1+F')(a-a_r)}\,da = \left(\frac{w_r}{M(1-e^{K'K})^n}\right)\left(\sum_{k=0}^{n}\frac{(-1)^k\binom{n}{k}e^{-kK'K}}{kK'+1+F'}\right). \quad \text{(A11)}$$

Substituting Equation A11 into Equation A6, multiplying through by MF', and differentiating gives the following expression:

$$\frac{dY(F')}{dF'}=MB(F')\left(1-\left(\frac{F'}{(1-q)\sum_{k=0}^{n}\frac{(-1)^k\binom{n}{k}e^{-kK'K}}{kK'+1+F'}}\right)\times\sum_{i}\frac{(-1)^k\binom{n}{k}e^{-kK'K}}{(kK'+1+F')^2}\right). \quad \text{(A12)}$$

Letting

$$z(F')=\frac{MB(F')}{(1-q)\left(\sum_{k=0}^{n}\frac{(-1)^k\binom{n}{k}e^{-kK'K}}{kK'+1+F'}\right)\prod_{k=0}^{n}(kK'+1+F')^2}, \quad \text{(A13)}$$

Equation A12 can be rewritten as

$$\frac{dY(F')}{dF'}=z(F')\left[\sum_{k=0}^{n}\left((-1)^k\binom{n}{k}e^{-kK'K}[(1-q)\times(kK'+1)-qF']\left(\prod_{m\neq k}(mK'+1+F')^2\right)\right)\right]. \quad \text{(A14)}$$

The term enclosed in large square brackets in Equation A14 can be expanded to polynomial form. Proceeding in steps, first note that

$$\prod_{m=0}^{n-1}(mK'+1)=\sum_{m=0}^{n-1}(-1)^m s(n,n-m)K'^m. \quad \text{(A15)}$$

Letting

$$\alpha_{k,m}=\sum_{\lambda=0}^{m}(-1)^{m+\lambda}(n-k)_\lambda s(n-\lambda,n-m) \quad \text{(A16)}$$

(except for $\alpha_{0,n}=n!$), Equation A15 can be extended to

$$\sum_{k=0}^{n}\left(\prod_{n\neq k}(mK'+1)\right)=\sum_{k=0}^{n}\left(\sum_{m=0}^{n}\alpha_{k,m}K'^m\right). \quad \text{(A17)}$$

Next, let

$$\beta_{k,l,m}=\alpha_{k,m}\binom{n-m}{l}, \quad \text{(A18)}$$

in which case Equation A17 can be extended to

$$\sum_{k=0}^{n}\left(\prod_{m\neq k}(mK'+1+F')\right)=\sum_{k=0}^{n}\left(\sum_{l=0}^{n}\left(\sum_{m=0}^{n}\beta_{k,l,m}K'^m\right)F'^l\right). \quad \text{(A19)}$$

Then, let

$$\gamma_{i,j,k}=\sum_{l=0}^{i}\left(\sum_{m=\max(0,\,j-n)}^{l}\beta_{k,l,m}\beta_{k,i-l,j-m}\right), \quad \text{(A20)}$$

in which case Equation A19 can be extended to

$$\sum_{k=0}^{n}\left(\prod_{m\neq k}(mK'+1+F')^2\right)=\sum_{i=0}^{2n}\left(\sum_{j=0}^{2n-i}\left(\sum_{k=0}^{n}\gamma_{i,j,k}K'^j\right)F'^i\right). \quad \text{(A21)}$$

Finally, the solution to Equation A14 can be written as a polynomial of degree $2n+1$ as follows:

$$\sum_{i=0}^{2n}\left[\sum_{j=0}^{2n-i}\left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}(k\gamma_{i,j,k}+\gamma_{i,j,k})e^{-kK'K}\right)K'^j - \left(\sum_{j=0}^{2n-i}\left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}(k\gamma_{i,j,k}+\gamma_{i,j,k}+\gamma_{i,j,k})e^{-kK'K}\right)K'^j\right)q\right]F'^{\,i}_{MSY} - \left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}e^{-kK'K}\right)qF'^{\,2n+1}_{MSY} = 0. \quad \text{(A22)}$$

In the special case where q=0, Equation A22 gives the following polynomial solution for F'_{max}:

$$\sum_{t=0}^{2n}\left[\sum_{t=0}^{2n-t}\left(\sum_{k=0}^{n}(-1)^k\binom{n}{k}(k\gamma_{t,j-1,k}+\gamma_{t,t,k})e^{-kK'K}\right)K'^{j}\right]F'^{t}_{max}=0. \quad \text{(A23)}$$

Equation A14 can be solved explicitly for q. The locus at which F'_{MSY}=1 is given by

$$q=\frac{\sum_{k=0}^{n}\left[(-1)^k\binom{n}{k}e^{-kK'K}\left(\prod_{m\neq k}(mK'+2)^2\right)(kK+1)\right]}{\sum_{k=0}^{n}\left[(-1)^k\binom{n}{k}e^{-kK'K}\left(\prod_{m\neq k}(mK'+2)^2\right)(kK+2)\right]}. \quad \text{(A24)}$$

Relationships between otolith microstructure, microchemistry, and early life history events in Dover sole, *Microstomus pacificus*

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Abstract.—Patterns of otolith microstructure and microchemistry (Sr/Ca ratios) are described in larval and juvenile Dover sole and related to developmental events and habitat. The initiation of metamorphosis is associated with a transition from clear (protein rich) to opaque (protein poor) material and formation of the first accessory primordium. Settlement is associated with the point at which growth from accessory primordia completely encloses growth from the central primordium and Sr/Ca ratio is minimal. No discrete otolith landmarks coincide with termination of metamorphosis.

Contrary to other flatfish that have a more abrupt metamorphosis, accessory primordia do not form until the left eye traverses the middorsal ridge of the cranium in Dover sole, an event that may occur months after the eye first reaches that position. A period of 70 days or more can separate the first- and last-formed accessory primordia in Dover sole, suggesting that all accessory primordia do not form in response to a single event.

A relationship between increments and days is validated for Stage 3–5 metamorphic and post-metamorphic stages. Duration of Stages 3 and 4 was in close agreement with predictions based on seasonal distributions. Duration of Stages 1 and 2, as determined by unvalidated increment counts, was about half as long as determined from seasonal distributions.

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Changes in otolith microstructure often correlate,and are presumed synchronous, with morphological and behavioral changes in larval and juvenile fish (Brothers and McFarland, 1981; Victor, 1982; Fowler, 1989; Ozawa and Penaflor, 1990; Gartner, 1991). The formation of secondary growth centers (accessory primordia) on flatfish otoliths is associated with metamorphosis in starry flounder, *Platichthys stellatus* (Campana, 1984a); plaice, *Pleuronectes platessa* (Alhossaini et al., 1989, Karakiri et al., 1989); California halibut, *Paralichthys californicus* (Kramer, 1991); and winter flounder, *Pseudopleuronectes americanus* (Sogard, 1991). Daily growth increments from accessory primordia are wider and are more likely composed of subdaily increments than those from the central primordium (Campana, 1984a; Karakiri et al., 1989; but also see Alhossaini et al., 1989).

Metamorphosis in flatfish includes a number of morphological and behavioral changes, most notably, eye migration and settlement from the water column to the sea floor. In most flatfish species, metamorphosis appears to be rapid; eye migration and settlement occur nearly simultaneously over a period of about 1 week (starry flounder, winter flounder, California halibut) to 3 weeks (plaice) (Ryland, 1966; Policansky, 1982; Campana, 1984a; Chambers and Leggett, 1987; Gadomski et al., 1992). Although timing of accessory primordium formation is not discussed in these studies, examination of published photographs suggests that the oldest and most recent accessory primordia are separated by only a few daily growth increments. In plaice, the earliest-formed accessory primordium (Alhossaini et al., 1989) or an unspecified accessory primordium (Karakiri et al., 1989) have been interpreted as settlement marks. In winter flounder, the earliest-formed accessory primordium has been interpreted as the point from which post-metamorphic age of an individual is determined (Sogard and Able, 1992). Counts and measurements of growth increments from accessory primordia to the otolith edge have been used to infer settle-

ment dates and post-settlement growth and mortality rates (Alhossaini et al., 1989; Karakiri et al., 1989).

In Dover sole (*Microstomus pacificus*), a commercially important northeast Pacific Ocean flatfish, metamorphosis differs from the rapid process described above. Markle et al. (1992) define five stages in Dover sole development. Stage 1 includes planktonic premetamorphic larvae from 6.1 to 58.5 mm standard length (SL). Eye migration begins when Stage-1 larvae are 10–15 mm SL but is arrested about midway through the process (Pearcy et al., 1977; Markle et al., 1992). Thus, Dover sole are optically asymmetrical during most of their planktonic life. Stage 2 includes planktonic metamorphic larvae from 42.3 to 60.4 mm SL, in which the eye has migrated past the mid-dorsal ridge and a pronounced shrinkage in body depth has begun. Stage 3 includes transitional metamorphic larvae from 40.7 to 74.9 mm SL, which are found in both the plankton and benthos. Stage-3 larvae are characterized by attainment of the adult configuration for a number of morphological characters. Stage 4 includes predominantly benthic, metamorphic larvae from 41.7 to 79.3 mm SL, which have formed a characteristic intestinal loop in the secondary body cavity. Stage 5 includes post-metamorphic juveniles from 48.9 mm SL to sexual maturity, which occurs at lengths greater than approximately 250 mm total length (Yoklavich and Pikitch, 1989; Hunter et al., 1992). Based on seasonal collections of staged larvae, Markle et al. (1992) estimated that duration of the metamorphic period (Stages 2, 3, and 4) is approximately 9 months.

The protracted metamorphic period in Dover sole provides an opportunity to examine changes in otolith structure and chemistry associated with each stage of metamorphosis. It may also be possible to distinguish between otolith landmarks associated with developmental processes and those associated with settlement from the water column to the bottom, because these events are not as coincidental in Dover sole as in other flatfish species. The objectives of this study were to 1) describe microstructure and microchemistry of Dover sole otoliths collected before, during, and after metamorphosis; 2) identify structural and chemical landmarks representing otolith growth during important morphological and behavioral transitions; 3) validate periodicity of increment formation in otoliths of metamorphic Stage-3 and Stage-4 larvae and post-metamorphic Stage-5 juveniles; and 4) using the otolith landmarks determined in objective 2 and increment counts between those landmarks and the otolith edge, re-examine the chronology of metamorphic events described in Markle et al. (1992).

Methods

Dover sole collections

Otoliths of six Stage-1, 103 Stage-3, 82 Stage-4, and 220 Stage-5 Dover sole were examined for microstructure and microchemical analysis. Specimens were obtained on various dates between 1987 and 1990 from bottom trawl collections off Oregon (Markle et al., 1992), opportunistic bottom trawl collections of commercial fishermen from Oregon and Washington, and midwater trawl collections off Oregon and central California[1] (Appendix 1).

The following measurements were taken to the nearest 0.1 mm on all specimens: standard length, body depth at anus (BD1A), and distance from snout to posterior extent of intestine (SINT). Weight of pat-dried specimens was determined to the nearest 0.1 g.

Otolith preparation and analysis for microstructure

Sagittae were removed after the fish were measured. Otoliths not immediately prepared for analysis were stored dry in vials. Terminology of otolith morphology follows Campana and Neilson (1985) and Secor et al. (1991), modified to account for features in Dover sole otoliths (Fig. 1 and Results section below). Left and right otoliths of Stage 3–5 Dover sole differ noticeably in shape (Fig. 1 and Results section below) and were analyzed separately.

The longest and shortest axes of sagittae from Stage-1 larvae were measured to the nearest 0.01 mm prior to mounting on slides in either a toluene-based medium (Histoclad) or an acrylic glue (Super Glue). Otoliths were then ground in the sagittal plane with 600-grit paper until growth increments became apparent.

Sagittae from Stage 3–5 Dover sole were cleaned in ethanol, air-dried, weighed to the nearest 0.01 mg, and measured along the anterior-posterior axis (maximum length) and along the dorsal-ventral axis (maximum width) to the nearest 0.01 mm (Table 1). The number of translucent rings (annuli) outside the clear central growth area (Fig. 1 and Results section below) was determined upon examination of whole otoliths under reflected light against a black background. Most otoliths were mounted on slides in a toluene-based medium (Histoclad) and the lateral face was ground in the

[1] Whipple, J. 1991. Progress in rockfish recruitment studies. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Center, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. T-91-01, 57 p.

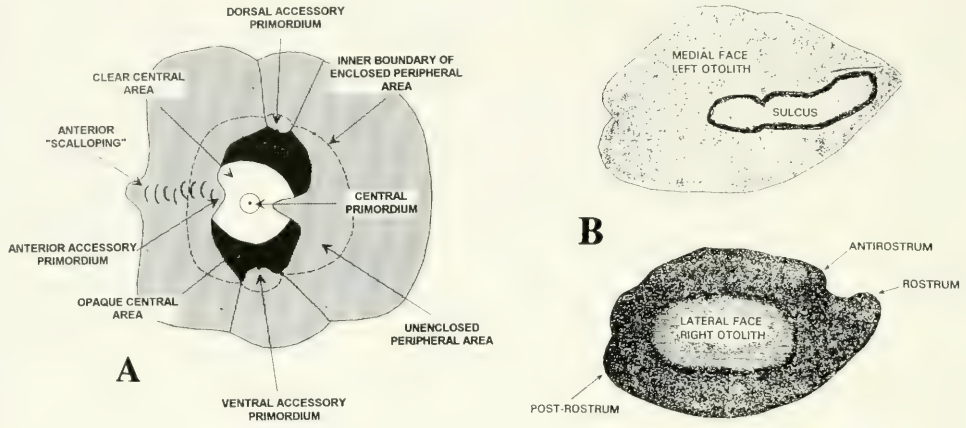

Figure 1

Schematic illustrations of Dover sole, *Microstomus pacificus*, otolith structure and orientation, showing terminology used in text. (**A**) Stage-4 left sagitta, sagittal section, lateral face towards the viewer, anterior to left. The anterior cavity is confluent with the anterior accessory primordium. (**B**) Orientation of left and right Stage-4 sagittae, anterior to right.

Table 1

Number of otoliths from Stage 3–5 benthic Dover sole, *Microstomus pacificus*, examined in study for each measurement or enumeration. AP = accessory primordium.

	Stage 3	Stage 4	Stage 5	Total
Right otoliths				
Whole otoliths				
Otolith length	81	53	215	349
Otolith width	81	53	215	349
Otolith weight	87	63	218	368
Number of annuli	87	63	209	359
Sagittal sections				
Diameter of clear central area	55	33	0	88
Number of AP	70	41	6	117
Increments since last AP (enclosed)	44	32	3	79
Increments since last AP (not enc.)	13	0	0	13
Increments since enclosure	51	46	3	100
Increments between checks	28	18	0	46
Left and right paired otolith comparisons				
Whole Otoliths				
Otolith length	67	50	198	315
Otolith width	67	50	196	313
Otolith weight	74	57	204	335
Sagittal sections				
Number of AP	41	22	0	63
Increments since last AP	23	12	0	35
First vs. last countable AP	14	11	0	25
Increments since enclosure	10	6	0	16
length anterior and posterior to AP	54	39	0	93

sagittal plane to the level of the central primordium. If resolution was not sufficient, the medial face was also ground to the central primordium. Otoliths from Dover sole >75 mm were ground and read progressively because all increments could not be observed in a single plane in sagittal section.

In order to examine otolith morphology in other planes, a subsample of otoliths from 17 Stage 3–5 Dover sole were embedded in low viscosity Spurr blocks (Haake et al., 1982) and ground to a level even with the central primordium in frontal or transverse sections. Ground sections were covered with a mounting medium and cover slip.

Additional otolith measurements were obtained from subsamples of Stage-3 and Stage-4 larvae (Table 1) to determine growth and development of features associated with metamorphic stages. The diameter of the clear central growth area (Fig. 1 and Results section below) of 88 right otoliths was measured to the nearest 0.02 mm on a black background at 50× with a dissecting scope and reflected light. Otoliths were then examined at 100, 400, and 1000× with a compound microscope and video monitor. At 100× we measured length of the otolith anterior and posterior to the central primordium to the nearest 0.01 mm in paired left and right otoliths from 93 larvae.

The number and position of accessory primordia, whether or not central primordium growth was completely enclosed by growth from accessory primordia, number of increments from accessory primordia to otolith edge, and number of increments from enclosure of central primordium growth to otolith edge were determined for all Stage-3 and Stage-4 larval otoliths in which the features were legible (Table 1). Similar information was obtained from 6 Stage-5 juveniles. Most counts and determinations were based on right otoliths; however, a subsample of left otoliths was also examined for paired comparisons (Table 1).

Counts of all growth increments from the first countable increment outside the central primordium to the otolith edge were made for five of six Stage-1 larval otoliths and for four Stage-3 larval otoliths exhibiting a variety of patterns of accessory primordium formation. Counts near the central primordium were made with 1000× light microscopy.

In all otoliths for which total increment counts were made and in approximately 20% of otoliths for which counts from accessory primordia were made, there were areas where accurate increment counts were not possible. In these areas, the number of increments was interpolated by linear approximation (Methot, 1983; Butler, 1989), based on the average widths of 5–20 increments on the distal or, preferably, both the proximal and distal sides of the uncountable area. Stage 3–5 larval otoliths with >5% interpolated increments were excluded from further analysis. We present the percentage of interpolated increments with total increment estimates for the few Stage-1 specimens examined.

Table 2
Rearing conditions of juvenile Dover sole, *Microstomus pacificus*, during the first validation experiment.

	Group 1	Group 2	Group 3
Collection depth	110 m	150 m and 163 m	108 m
Number injected	4	10	21
Number controls	13	0	0
Average weight[1]	5.4 g	3.4 g	4.5 g
Aquarium volume	152 L	76 L	114 L
Average density	0.036 g/L	0.045 g/L	0.039 g/L
Temperature	8°C	10°C	12°C

[1]Average for entire experiment, based on weights at death.

Validation of increment deposition rate

Two groups of juvenile Dover sole were given interperitoneal injections with a solution of 0.01 g oxytetracycline hydrochloride (OTC)/mL distilled water at a dose of 0.1 g OTC/kg fish weight (Campana and Neilson, 1982) to produce fluorescent marks on their otoliths. Dover sole in the first experimental group were held at three constant temperatures to evaluate temperature effects on increment formation. Those in the second experimental group were exposed to identical temperatures and were injected once in March and again in September to evaluate seasonal effects on increment formation.

First experiment An initial group of 48 juvenile Dover sole was collected at four stations off Cape Foulweather, Oregon, on 17 March 1990 (Table 2). Thirty-five fish were injected on that day and 13 served as uninjected controls to check for naturally occurring fluorescence. The fish were held in aquaria containing artificial seawater (Instant Ocean) and fed to satiation with *Tubifex* worms once per day in the morning. Fluorescent lights in the room were set to natural cycles, and aquaria were partially covered to reduce incoming light. Rearing conditions are summarized in Table 2.

Fish were sacrificed 21 (n=6), 26 (n=4) or 29 (n=9) days following initial injection. The remaining 29 fish were given a second injection of OTC 36 days after capture and were sacrificed 5 (n=6), 8 (n=10), or 12 (n=13) days after the second injection (i.e., 41, 44, or 48 days after initial injection).

Second experiment A second group of 10 juvenile Dover sole ranging from 55.3 to 118.3 mm was collected on 20 March 1991 at 77 m off Cape Foulweather, Oregon, and injected the following day. The fish were held in a flow-through filtered seawater tank. Ambient nearshore oceanic water entering the tank averaged 10.7°C (range: 8.7–14.6°C) during the experiment. Fish were exposed to diffused natural light and fed as in the first experiment. Seven days after injection, four fish, 55.3–63.9 mm, were sacrificed. The remaining six fish were individually marked with fin clips on 27 April. They were re-injected on 11 September, 174 days after first injection, and sacrificed 19 days later. Lengths ranged from 88.2 to 152.2 mm.

Otoliths from both groups of fish were prepared as described above and examined at 100–1000× on a Zeiss microscope equipped with a IV Fl epifluorescence condenser. The preparation was examined under full spectrum light to locate areas with distinct growth increments and the OTC band was then observed under ultraviolet light.

At least two documentary 35-mm slides of each otolith were taken: one showing the fluorescent band as well as the otolith edge and one showing increments under full-spectrum illumination. Each slide was projected and traced onto the same sheet of paper, resulting in a diagram that showed the location of the fluorescent band in relation to increments and other landmarks. The diagram served as documentation for increment counts as well as a guide for further examination with light microscopy. Photographs and counts were made at one to four locations on each otolith, usually at the rostrum, antirostrum, or post-rostrum (Fig. 1). Increment counts were generally made on right otoliths; left otoliths were used only if right otoliths were unavailable or illegible. All otoliths were read at least twice on separate dates by the same reader and the average was used in subsequent analyses. The range of estimates for each otolith and standard deviation of mean counts were also determined.

Results were analyzed by regressing number of increments between the proximal edge of the innermost fluorescent band and edge of the otolith against number of days since OTC injection. When a second fluorescent band was obvious and the area distal to the second band was illegible, counts were made between bands. To determine if all experimental groups could be combined into one regression, multiple regressions, including "dummy variables" corresponding to experimental groups, were analyzed with partial F-tests (Neter et al., 1989:364–370). The slope of the final regression model was compared to a slope of 1.0 (Neter et al., 1989).

Otolith preparation and analysis for microchemistry

Otoliths from two Stage-3 larvae (51.3 and 61.9 mm), three Stage-4 larvae (54.6, 57.1, and 65.7 mm), and two Stage-5 juvenile Dover sole (88.6 and 172.2 mm) were examined with a wavelength dispersive electron microprobe to determine if microchemical changes were associated with microstructural changes. Preparation and analytical techniques followed Toole and Nielsen (1992). Beam diameter was 5 µm, counting time for each element was 20 seconds, accelerating voltage was 15 kV, and current was 20 nA.

Results

Validation of increment deposition rate

First experiment Otoliths from uninjected control fish exhibited bright yellow-green fluorescence around the edge of the otolith and weaker fluorescence associated with strong checks and scratches. However, fluorescent marks observed on injected fish differed markedly in appearance. Twenty-seven injected fish had at least one otolith with one or two distinct fluorescent bands located inside the otolith edge (Fig. 2, A and B). Fluorescent bands extended over two to six increments.

Increments formed after capture were often less distinct than those formed in nature (Fig. 3), and four of 27 injected fish with fluorescent bands (14.8%) had otoliths with such poorly defined increments that they were considered unreadable and were eliminated from further analysis.

Both daily and subdaily increments (Campana and Neilson, 1985) were observed. For those otoliths in which both subdaily and larger increments could be counted in the same area, the ratio of small to large increments averaged 2.78 (n=10 fish, range 1.36–3.48). In most cases, larger growth increments could easily be distinguished from subdaily increments by adjusting the focus. However, in otoliths of two fish (7.4% of those with fluorescent bands), only subdaily increments could be observed. These fish were also eliminated from further analysis.

Second experiment Four Dover sole sacrificed 7 days after first injection had not fed. The remaining six fish began feeding approximately two weeks after the first OTC injection. Two of these fish grew rapidly throughout the experiment, whereas the other four fish ceased growing after about 20 weeks (Fig. 4).

Two of four Dover sole sacrificed 7 days after first injection and five of six fish sacrificed 19 days after second injection had at least one otolith with a

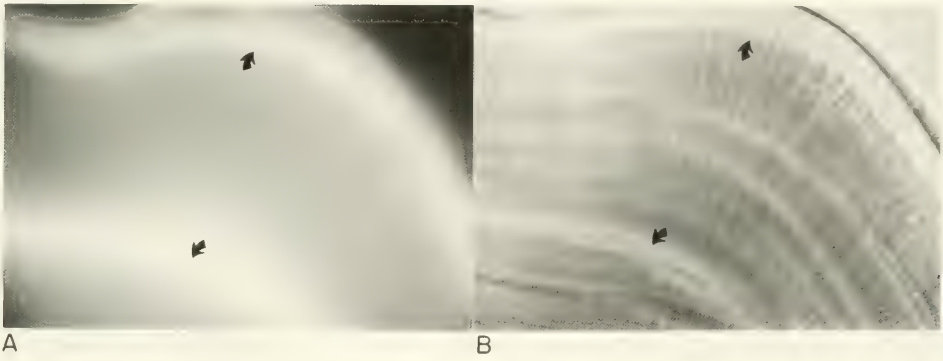

Figure 2

Sagittal section of right otolith from 67.2 mm Stage-4 Dover sole, *Microstomus pacificus*, larva marked with OTC and held in a 12°C aquarium for 48 days. Magnification = 400×. (**A**) Photograph taken with ultraviolet light; arrows show fluorescent OTC marks. (**B**) Same preparation taken with full-spectrum light; arrows show position of fluorescent OTC marks.

fluorescent mark and countable increments (70% of injected fish). Increment width was narrow, ranging from 0.63 to 1.88 μm. Because all counts underestimated the true number of days since injection and because larger marks were not apparent by adjusting focus, the marks were not equivalent to subdaily marks observed in the first experiment. The OTC mark deposited after first injection was not visible in fish held until second injection, so increments deposited during the entire 183-day period could not be counted.

Precision of counts Maximum and minimum increment counts for each otolith differed from mean counts by an average of 5.7% (Range=0–20%). Standard deviations associated with mean increment counts averaged 1.84 (Range=0–7.8).

Validation relationships Neither variances (Bartlett's test, B=1.48, P=0.11) nor mean observed/expected increment counts (ANOVA, df=27, F=2.21, P=0.10) differed between the five experimental groups of fish (three aquarium temperatures in the first experiment, March and September marking groups in the second experiment). Similarly, regressions of observed versus expected counts did not improve when a model containing separate slopes and intercepts for each experimental group was compared with a model containing separate intercepts and one slope (F=0.313, df=5,22,

Figure 3

Left otolith, anterior end of frontal section; from 68.0 mm Stage-4 Dover sole, *Microstomus pacificus*, larva marked with OTC and held in a 10°C aquarium for 44 days. Arrow marks capture point, as identified by OTC fluorescence. Increments prior to capture are well-defined, whereas increments formed in aquarium are nearly indiscernible. Magnification = 400×.

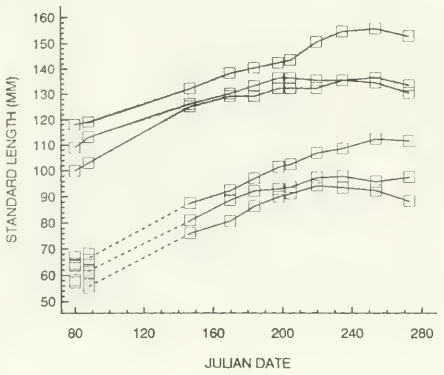

Figure 4

Relationship between standard length and calendar date of Dover sole, *Microstomus pacificus*, held in an ambient flow-through seawater tank, 21 March–30 September 1991 (Julian dates 80–272). Smaller fish were not marked initially; dotted lines indicate uncertainty regarding growth trajectories.

P=0.899) or when the model with separate intercepts and one slope was compared with a model containing one slope and one intercept (F=1.14, df=5,22, P=0.369), so all experimental groups were initially combined into one regression. However, inspection of residuals from that regression suggested that a greater error was associated with counts from Stage-5 juveniles than with counts from Stage-3 and Stage-4 larvae, regardless of experimental group. Mean ratios of observed:expected counts for fish <80 mm (0.924) than for fish ≥80 mm (0.718) (t-test, df=26, P=0.012). Therefore, each size group was treated separately in the final regression models.

The relationship for Dover sole <80 mm was

Days since marking = 3.81 + (0.962 * observed increments),

where n=21, r^2 = 0.85, $SE_{INTERCEPT}$ = 2.90, and SE_{SLOPE} = 0.091 (Fig. 5A). The calculated slope was not significantly different from 1.0 (t=0.419, df=26, P=0.34); however, the power of this test (Peterman, 1990) was too weak to conclude that increments were deposited daily (1–ß≈0.06; Rice, 1987, Neter et al., 1989).

The relationship for Dover sole ≥80 mm was

Days since marking = 6.32 + (1.026 * observed increments)

where n=7, r^2 = 0.93, $SE_{INTERCEPT}$ = 2.81, and SE_{SLOPE} = 0.122 (Fig. 5B). The calculated slope was not significantly different from 1.0 (t=0.211, df=6, P=0.42); however, the power of this test was also too weak to conclude that increments were deposited daily (1–ß≈0.05).

Error in the preceding regressions was due, in part, to poor resolution of laboratory-formed increments (Fig. 3; Campana and Neilson, 1985) and may therefore be greater than the error associated with ageing wild-captured fish. However, several resolution problems appeared common to otoliths of wild-captured and laboratory-reared fish: difficulty interpreting increments at the otolith margin, difficulty resolving increments around stress checks (Campana and Neilson, 1985) in certain regions of the otolith because of compression (and sometimes fusion) of increments, and occasional difficulty distinguishing daily and subdaily increments. For these reasons, use of both slope and intercept estimates was considered reasonable when back-calculating days from increments in otoliths of wild-captured fish. The same relationships were applied to increment counts outside the range of observations, which may introduce an unavoidable source of additional error.

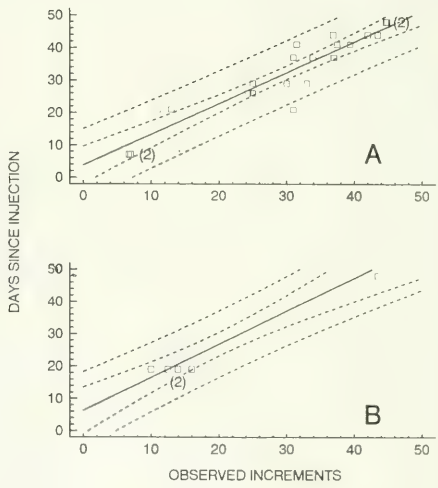

Figure 5

Relationship between days since OTC injection and number of growth increments in Dover sole, *Microstomus pacificus*, otoliths. Inner dashed lines are 95% confidence limits for mean response; outer dashed lines are 95% prediction limits. (**A**) Relationship for Stages 3 and 4 <80 mm SL. Formula: days since injection = 3.81 + (0.96 * observed increments); n=21; r^2=0.85. (**B**) Relationship for Stage-5 Dover sole ≥80 mm SL. Formula: days since injection = 6.32 + (1.03 * observed increments); n=7; r^2=0.93.

Table 3

Characteristics of five Stage-1 Dover sole, *Microstomus pacificus*, otoliths. Number of increments equals number observed plus number interpolated by linear approximation. The range of values presented for one larva reflects uncertainty in interpreting possible subdaily increments.

Standard length (mm)	Collection date	Maximum diameter (mm)	Number of increments	Percent interpolated (%)	Mean increment width (μm)
30.1	January, 1987	0.10	77	52	1.30
20.6	March, 1991	0.15	103	33	1.46
46.0	July, 1991	0.25	160–180	0	1.39–1.56
51.5	July, 1991	0.28	229	20	1.22
47.7	Oct., 1991	0.30	182	5	1.64

Structural patterns

Growth from central primordium Two prominent areas were seen within the field of growth emanating from the central primordium.

Clear central area Stage-1 larval otoliths were translucent and hemispheric (appearing nearly circular in sagittal section), with all growth emanating from the central primordium (Figs. 1 and 6). The left eye had previously migrated to the dorsal ridge of the cranium in all Stage-1 larvae examined. The diameter of Stage-1 larval otoliths ranged from 0.10 to 0.30 mm and the number of increments ranged from 77 to 229 (Table 3). When fully formed in Stage-3 larval otoliths, this clear central area was 0.24–0.49 mm (mean=0.39, n=60) and contained 187–230 increments (Table 4). Mean increment width in the clear central growth area ranged from 1.22 to 1.56 μm, and increment widths nearer the central primordium were approximately 0.5 μm, suggesting that, when counting increments, underestimation may have occurred owing to resolution limitations of light microscopy (Campana et al., 1987).

A structural feature of some Stage-1 larval otoliths was the presence of one or two conical cavities, which radiated towards the anterior and posterior edges (Fig. 7). Each cavity was enclosed laterally and medially and was open at the anterior or posterior end. The anterior cavity may be continuous with the sulcus, which was visible on one Stage-1 larval otolith.

Opaque central area An opaque area surrounded and was continuous with the clear central area in all Stage 3–5 larval otoliths (Figs. 1 and 8, A–D). Increments in this region were wider than increments in the clear central area (1.6–1.8 μm) and there was higher contrast between continuous and discontinuous zones within increments. Continuity of increments was interrupted by the conical cavities described previously and by accessory primordia. The number of increments in this area ranged from 46 to 95 (Table 4).

Growth from accessory primordia We recognized two zones of growth from accessory primordia, distinguished by the point at which growth from the central primor-

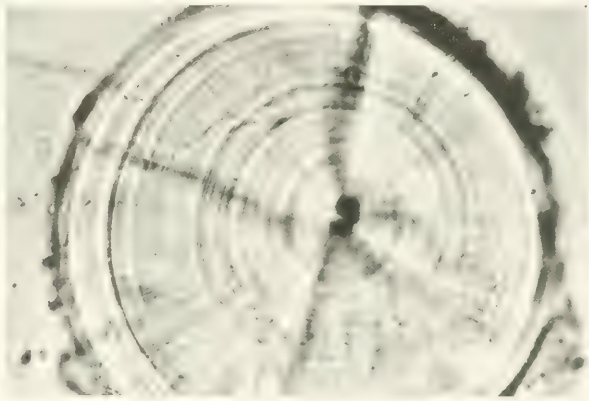

Figure 6

Sagitta from 20.6 mm Stage-1 Dover sole, *Microstomus pacificus*, larva collected on 1 April 1990 at NMFS Station 9003-35. Estimated number of increments was 103 (Table 3). Magnification = 1000×.

Table 4

Increments counted from central primordium to structural landmarks on four Stage-3 Dover sole, *Microstomus pacificus*, otoliths shown in Figure 8, A–D. Assigned dates (in parentheses) are determined from the increment:day regression for growth distal to accessory primordia. Periodicity of increments proximal to accessory primordia has not been validated. Ranges indicate uncertainty interpreting possible subdaily increments or determining exact location of the clear to opaque transition. The first distinct accessory primordium is not the first-formed accessory primordium. NP = not present; AP = accessory primordium.

	Standard length of larvae (mm)			
Landmark	55.6	46.9	64.9	55.5
Central primordium	0	0	0	0
Clear to opaque transition	187–213	205–219	≈230	≈200
First distinct AP	196–222 (19 Nov. 88)	NP	322 (3 Dec. 89)	206 (17 Dec. 89)
Last AP	224–250 (16 Dec. 88)	NP	338 (18 Dec. 89)	222 (1 Jan. 90)
Central primordium enclosure	NP	300–314 (20 Feb. 90)	376 (24 Jan. 90)	252 (30 Jan. 90)
Otolith edge	255–281	322–336	425	296
Capture date	19 Jan. 89	17 Mar. 90	17 Mar. 90	17 Mar. 90

dium was completely enclosed. This determination is based on sagittal sections at the level of the central primordium.

Unenclosed peripheral area

Otoliths of all Stage 3–5 larvae had at least two accessory primordia (AP), when viewed in sagittal section (Fig. 8, A–D). A maximum of seven AP were observed, although additional AP on the lateral surface of the otolith (Fig. 9) were obscured when otoliths were prepared in sagittal section. Accessory primordia always formed adjacent to growth from the central primordium, rather than adjacent to growth from previously formed AP. On right otoliths, AP were easier to discern than on left otoliths, possibly because the plane of growth changes at about the time of AP formation in left, but not right, otoliths (Fig. 10, A and B). Increments emanating from AP exhibited higher contrast and were wider (about 3.0 μm) than those emanating from the central primordium.

The most anterior AP appeared to form first and was closely associated with the transition from clear to opaque central areas. However, the exact origin of the anterior AP was usually impossible to discern because it merged

Figure 7

Sagitta from 51.5 mm Stage-1 Dover sole, *Microstomus pacificus*, larva collected on 12 July 1991 near Destruction Island, Washington. Anterior and posterior cavities are indicated by arrows. The lateral face of the otolith (surface toward viewer) has been ground to the level of the central primordium; the medial face has been left intact. Estimated number of increments was 229 (Table 3). Magnification = 400×.

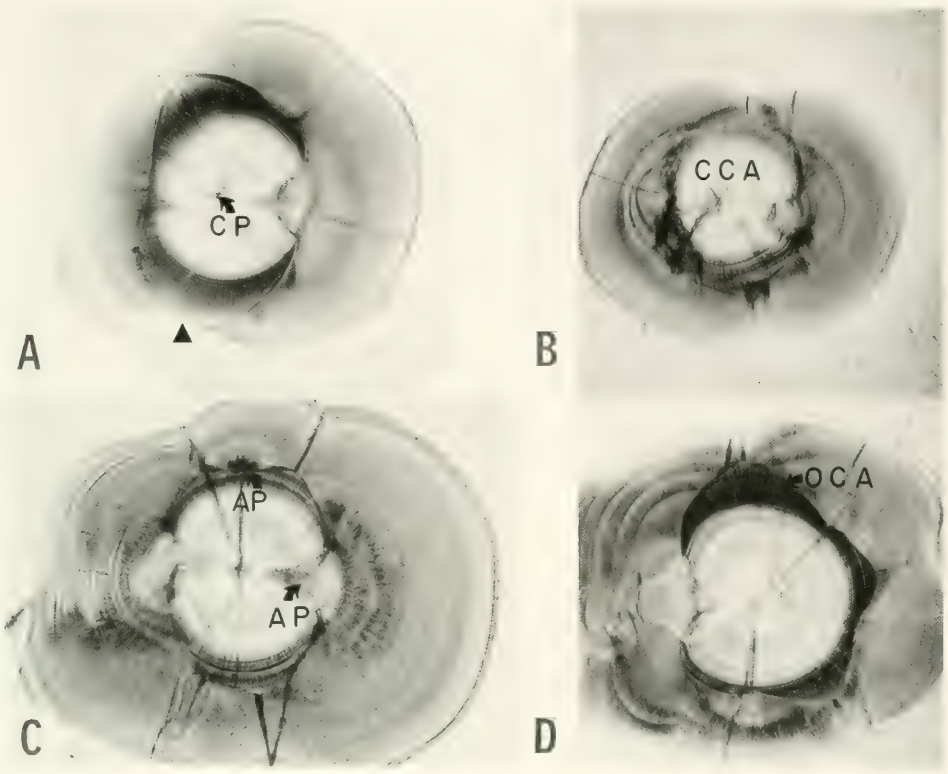

Figure 8

Stage-3 Dover sole, *Microstomus pacificus*, otoliths showing variations in accessory primordium formation; anterior to left, dorsal toward top in A–C, dorsal toward bottom in D. AP = accessory primordium, CCA = clear central area, CP = central primordium, OCA = opaque central area. (**A**) Left otolith of 55.6-mm larva collected 19 January 1989, showing unenclosed central primordium growth (indicated by triangle). Magnification = 100×. (**B**) Left otolith of 46.9-mm larva collected on 17 March 1990, showing two accessory primordia (anterior and posterior) completely enclosing growth from the central primordium. Magnification = 100×. (**C**) Left otolith of 64.9-mm larva collected 17 March 1990, showing growth from four accessory primordia (anterior, posterior, dorsal, and ventral) completely enclosing growth from the central primordium. Magnification = 100×. (**D**) Right otolith of 55.5-mm larva collected on 17 March 1990, showing growth from four accessory primordia (one anterior, two posterior, and one dorsal) completely enclosing growth from the central primordium. Magnification = 100×.

with the conical cavity described previously (Fig 8, A–D). This situation also applied to the origin of the most posterior AP in left otoliths (Fig. 8, A–C). The chronology of additional AP formation did not follow a consistent pattern. Dorsal and ventral AP were often associated with dark bands in the opaque central area (Fig.11).

Dorsal and ventral AP were formed 196–338 increments distal to the central primordium (Table 4). When increments were counted back from the otolith edge, dates of last AP formation varied between fish, ranging over a six-month period from October to March (Fig. 12). The number of days between the first-formed and last-formed dorsal and ventral AP averaged 28.8 (range 1–75, n=25). This range would be greater if it were possible to make accurate counts to the anterior AP.

Enclosed peripheral area Growth from accessory primordia completely enclosed growth from the cen-

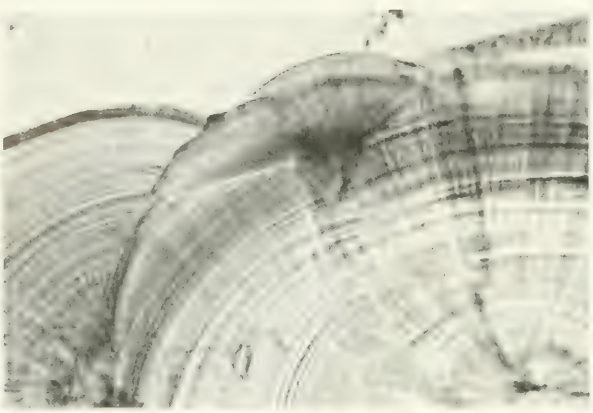

Figure 9

Transverse section of right otolith of 47.5-mm Stage-3 Dover sole, *Microstomus pacificus*, larva collected on 22 March 1989, showing recently-formed accessory primordium near medial surface (toward top) that would be undetectable in sagittal section. Magnification = 400×.

tral primordium in at least one otolith of 78% of benthic and 71.4% of pelagic Stage-3 larvae, 98.4% of benthic and 100% of pelagic Stage-4 larvae, and 100% of Stage-5 larvae, suggesting that most otoliths were enclosed before or during Stage 3. Enclosure of growth from the central primordium occurred an average of 33.7 days after formation of the last accessory primordium (range 0–87, n=108).

During Stages 3 and 4, SINT increases as the intestinal loop extends into the secondary body cavity and BD1A decreases as body depth shrinks (Markle et al., 1992). Consequently, fish with low SINT/BD1A ratios are presumably at an earlier stage in the metamorphic process than fish with higher ratios. Benthic Stage-3 larvae with at least one unenclosed otolith had a lower ratio of SINT/BD1A (mean=1.06) than benthic Stage-3 larvae with enclosed otoliths (mean=1.15) (t-test, df=46, P=0.0096), as did pelagic Stage-3 larvae (0.90 vs. 1.32, t-test, df=28, P=0.019), suggesting that Stage-3 larvae with unenclosed otoliths were at an earlier stage of development than Stage-3 larvae with enclosed otoliths.

Stage-3 larvae with enclosed otoliths were collected an average of 24.4 days after enclosure (range= 5.7–65.4, n=51) while Stage-4 larvae in the same collections averaged 51.9 days (range=9.6–125.9, n=46). The difference (27.5 days) may represent the average duration of Stage 3.

Otolith elongation along the anterior-posterior axis became more pronounced following enclosure, as did asymmetry between left and right otoliths. Left otoliths were heavier (paired t-test, df=335, P<0.001), longer (paired t-test, df=314, P<0.001) and wider (paired t-test, df=312, P<0.001) than right otoliths. In addition, the proportion of otolith length anterior to the central primordium was higher in right than left otoliths (t-test, df=92, P<0.001) by an average of 8.5% (Fig. 8, A–D). The number of accessory primordia tended to be higher on right than on left otoliths (paired t-test, df=62, P=0.036), while more increments formed after the last AP (paired t-test, df=34, P=0.006) and after the point of enclosure (paired t-test, df=15, P=0.011) on left than on right otoliths.

Stress checks became prominent in sagittal section following enclosure (Fig. 8, B–D). Enumeration of stress checks and determination of periodicity was difficult because checks were often discontinuous around the otolith and, even when continuous, the number of observable increments between checks varied regionally. However, mean periodicity of check formation in 46 Stage-3 and Stage-4 otoliths collected over a three-day period in March, 1990, suggested synchrony of check formation in otoliths of different fish and regularity in periodicity of check formation (Fig. 13). Calculated dates of check formation did not correspond to particular lunar phases. Number of days between checks ranged from 5.7 to 33.6, with a mode of 12.5 days and an average of 15.3 days (Fig. 14).

Other features of the enclosed peripheral zone in older fish were the development of a rostrum (Figs. 1 and 15) and formation of translucent growth zones (Fig. 16). All Stage-5 otoliths collected in January and March had at least one translucent growth zone. This first post-settlement translucent growth zone was initiated in late fall of the settlement year (240–293 days after formation of the last AP) and was completed the following spring (125 to 141 days later) in otoliths of three Stage-5 juveniles. Based on daily increment counts and seasonal deposition patterns, the first and subsequent translucent growth zones are interpreted as post-settlement annuli formed during slow winter growth periods (Fig. 17, page 746). This interpretation is consistent with Hagerman (1952) and Chilton and Beamish (1982).

Although there was little difference in weight between the largest Stage-4 and smallest Stage-5 Do-

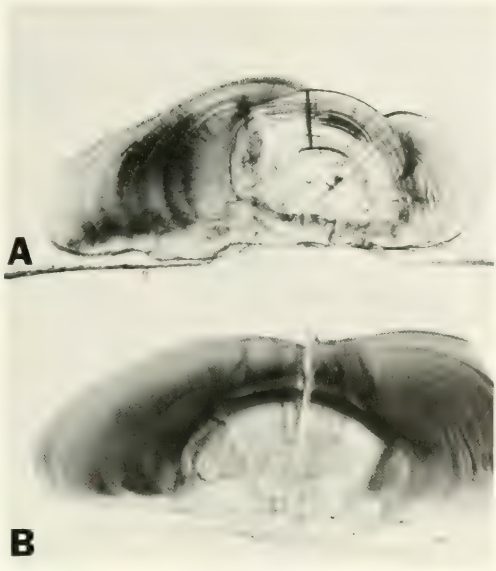

Figure 10

Frontal sections of left and right Dover sole, *Microstomus pacificus*, otoliths showing differences in orientation of the clear central growth area; anterior to right, lateral surface to top. (**A**) Left otolith from 58.0-mm Stage-3 larva collected on 16 March 1990. Central area tilts towards the lateral surface posteriorly and towards the medial surface anteriorly. (**B**) Right otolith from 64.9-mm Stage-3 larva collected on 17 March 1990. Central area is oriented in the same direction as surrounding peripheral growth.

ver sole collected in January and March, otolith weight in Stage-5 juveniles was nearly double that of Stage-4 larvae (Fig. 18, page 746). A discontinuity in the relationship between Stage 3–5 right otolith length and fish length during the first winter following settlement was also apparent (Fig. 19, page 746). This relationship was best described by a three-stanza segmented linear model (Bacon and Watts, 1971; Laidig et al., 1991). Parameter estimates in Table 5 (page 746) resulted in a good fit (r^2=0.955) and no discernable pattern in residuals. The first segment consisted of Stage-3 and Stage-4 larvae; the second, of Stage-4 larvae and Stage-5 juveniles; and the third, of only Stage-5 juveniles.

Microchemical patterns

Ratios of Sr/Ca exhibited similar patterns along transects through the otoliths of all larvae and juveniles examined (Figs. 20, A–B, page 747, and 21, page 748). An initial Sr/Ca spike (0.007–0.010) occurred approximately 48 μm from the central primordium, inside the clear central area. Following the spike, Sr/Ca levels within the clear central area fluctuated at intermediate levels (0.004–0.006). Sr/Ca ratios began a second, more gradual, decline beginning near the clear-to-opaque transition in the central area of the otolith, which also corresponded to the area in which the anterior AP was forming. This decline began in late summer or fall of the calendar year prior to settlement.

Sr/Ca ratios often reached minimum levels following formation of accessory primordia. In a 65.7-mm Stage-4 larval otolith (Fig. 20A), Sr/Ca ratios reached a minimum (0.002) at about the end of January. This minimum point was approximately 10 days beyond enclosure of growth from the central primordium and 31 days beyond the most recently formed accessory primordium. In a second Stage-4 larva, a minimum (0.003) was first reached in mid-De-

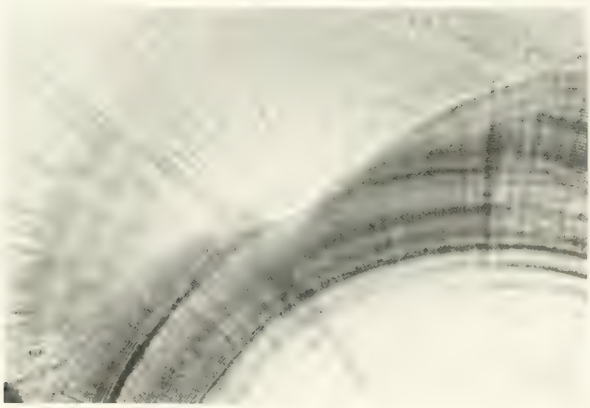

Figure 11

Posterior accessory primordium on right otolith of 58.0-mm Stage-3 Dover sole, *Microstomus pacificus*, larva collected on 16 March. Narrow dark band in the opaque central area is associated with origin of the accessory primordium. Magnification = 400×

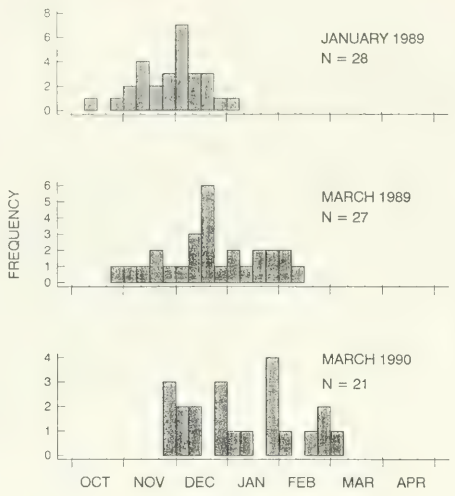

Figure 12

Dates of last accessory primordium formation on right otoliths of Stage-3 and Stage-4 Dover sole, *Microstomus pacificus*, larvae collected during three sampling cruises in 1989 and 1990. Only enclosed otoliths with three or more accessory primordia were considered because origins of single anterior and posterior accessory primordia are usually indistinct.

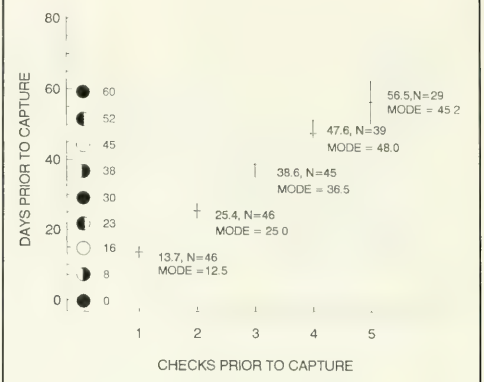

Figure 13

Relationship between the five most distal stress checks and number of days from their formation to the otolith edge (capture) in 46 Stage-3 and Stage-4 Dover sole, *Microstomus pacificus*, otoliths collected between 15–17 March 1990. Vertical bars represent 95% confidence intervals for means (horizontal bars). Additional error is associated with converting increments to days, with the regression described in the text. Corresponding lunar phases are displayed on the vertical axis.

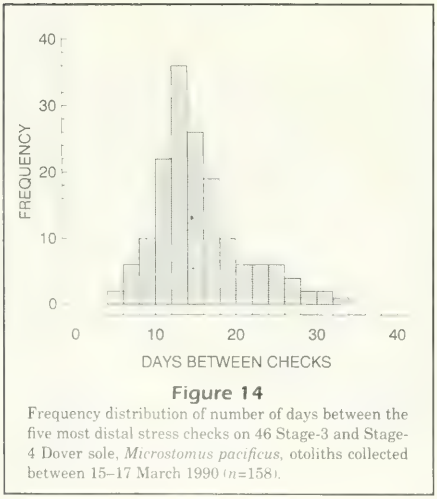

Figure 14

Frequency distribution of number of days between the five most distal stress checks on 46 Stage-3 and Stage-4 Dover sole, *Microstomus pacificus*, otoliths collected between 15–17 March 1990 (n=158).

cember. The ratio then rose and fell to a second minimum (0.003) in mid-January. In each of these larvae, the ratio rose again (0.003–0.0035) prior to capture in mid-March. Two Stage-3 larvae and a third Stage-4 larva did not exhibit distinct minima; rather, Sr/Ca ratios remained at about 0.0025 until capture. Sr/Ca ratios first reached this level prior to enclosure.

An 88.6-mm Stage-5 juvenile (Fig. 20B) with one peripheral annulus had narrow growth increments, making it difficult to determine exact ages associated with microprobe samples. However, the pattern proximal to AP was similar to that of larvae, with one 0.007 spike and a 0.004–0.006 peak near the center of the otolith, followed by a decline occurring prior to and during formation of accessory primordia. Sr/Ca ratios remained low for >200 days following formation of the last AP until a second 0.004–0.005 peak formed in the translucent annulus near the otolith edge, which represented capture in March.

A 172.2-mm juvenile, collected in November 1989 and judged to have three complete post-settlement annuli and a fourth one forming, had four Sr/Ca peaks, which corresponded to translucent annuli (Fig. 21), distal to accessory primordia.

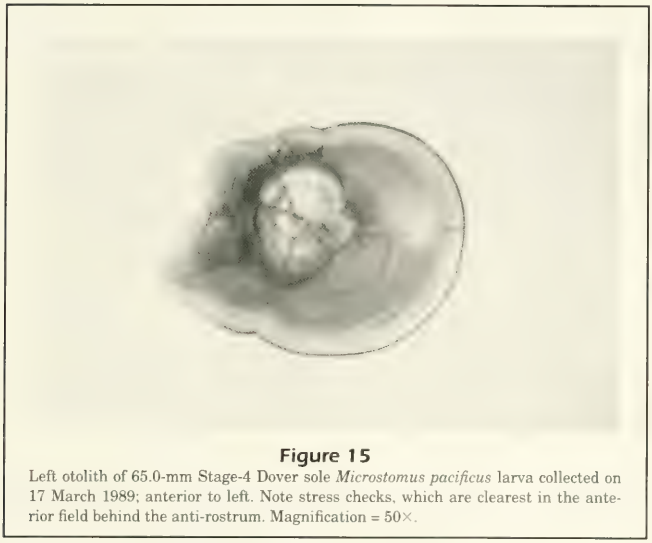

Figure 15
Left otolith of 65.0-mm Stage-4 Dover sole *Microstomus pacificus* larva collected on 17 March 1989; anterior to left. Note stress checks, which are clearest in the anterior field behind the anti-rostrum. Magnification = 50×.

Discussion

Relation of otolith microstructure to metamorphic stages

Premetamorphic larvae Sagittal otoliths of Stage-1 larvae between 20.6 and 51.5 mm were uniformly translucent and lacked accessory primordia. Since the left eye had migrated to the middorsal ridge of the cranium in each specimen, formation of AP is not triggered by the initiation of eye migration or movement to this position in Dover sole. Cavities noted in Stage-1 larval sagittae have not been described previously and their derivation and function are unknown.

Metamorphic larvae Because Stage-2 larval otoliths were not available, the transition from clear to opaque central areas and development of the first two accessory primordia cannot be attributed to this stage with certainty. However, because neither of these features were developed in Stage-1 larval otoliths, yet both were present in all Stage-3 larval otoliths, it is probable that they formed during Stage 2. Thus, the transition from clear to opaque growth and initiation of AP formation occur after the left eye moves beyond the dorsal ridge and metamorphosis (as defined in Markle et al., 1992) begins, but before larvae are first collected on the bottom.

Formation of the first accessory primordium in plaice and winter flounder also does not occur until the left eye has migrated at least to the dorsal ridge of the cranium (Alhossaini et al., 1989; Sogard, 1991). However, unlike Dover sole, AP in otoliths of these species can form before the eye has moved past that point. Comparisons with other flatfish species are more difficult. Accessory primordia form "at or shortly after metamorphosis" in starry flounder (Campana, 1984a) and "after metamorphosis" in California halibut (Kramer, 1991); however, the definition of metamorphosis relative

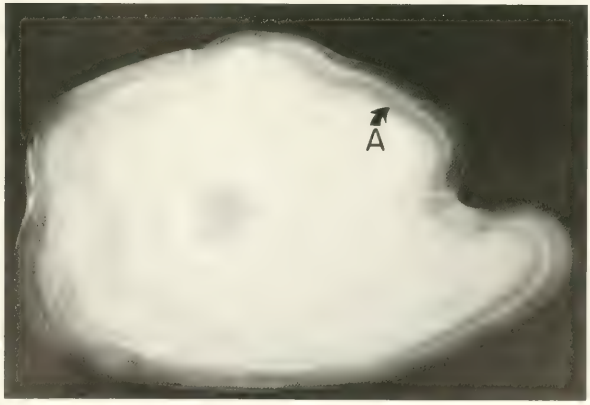

Figure 16
Right otolith of 100.4-mm Stage-5 juvenile Dover sole, *Microstomus pacificus*, caught on 18 March 1991 (anterior to right), photographed with reflected light against black background. Note the first annulus, which appears darker than the inner area. Magnification = 50×. A = annulus.

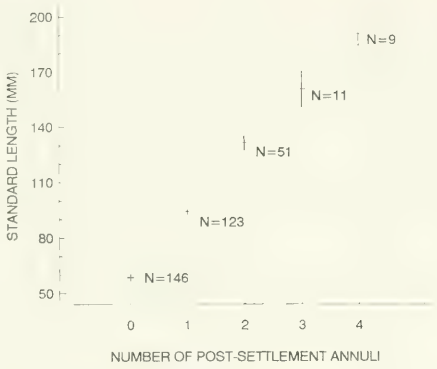

Figure 17

Relationship between standard length and number of post-settlement annuli in Dover sole, *Microstomus pacificus*, collected in January 1989, March 1989, and March 1990. Vertical bars represent 95% confidence intervals for means (horizontal bars).

to cranial morphology was not specified in these studies.

Formation of accessory primordia has also been noted in several non-pleuronectiform taxa (Brothers, 1984). Gartner (1991) described a clear to opaque transition with accompanying formation of AP in otoliths of myctophid species and suggested these features were

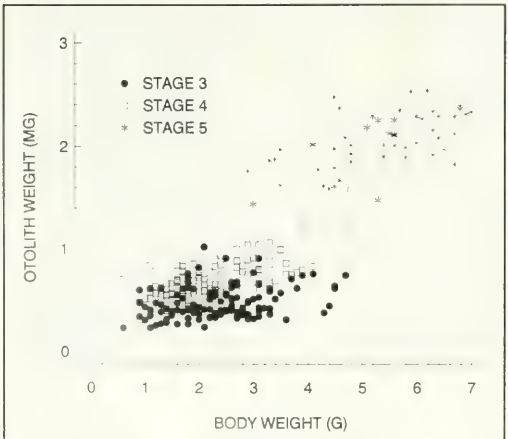

Figure 18

Relationship between weight of right otolith and body weight in Stages 3–5 Dover sole, *Microstomus pacificus*. Note change in the relationship during the transition from Stage 4 to Stage 5 (n=368)

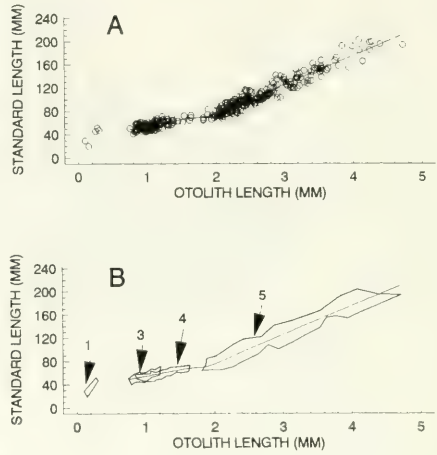

Figure 19

(**A**) Relationship between standard length and right otolith length in Stages 3–5 Dover sole, *Microstomus pacificus*. Formula and parameter estimates are included in Table 5. n = 351; r^2 = 0.955. Points representing standard length and right otolith diameter of five Stage-1 larvae are also included. While Stage-2 otoliths were not available, it appears that otolith length increased between Stage 1 and Stage 3, whereas fish length did not. (**B**) Polygons circumscribing areas bounded by fish in Stages 1 and 3–5.

Table 5

Estimated parameters for segmented linear regression model of the form

$$\text{Standard Length (mm)} = e + d_1(x-c_1) + d_2(x-c_1)s_1 + d_3(x-c_2)s_2,$$

where x = right otolith length (mm), $s_i = [2*(1/(1+\exp(-[x-c_i]/0.1)))]-1$ (i.e., the logistic cumulative distribution function, used as a transition function between segments, with the constant 0.1 specifying a rapid transition between segments), c_i = fitted inflection points, and e and d_i = fitted parameters (n = 351, r^2 = 0.955).

Parameter	Estimate	Standard error
e	63.753	36.999
c_1	1.640	1.045
c_2	1.891	0.230
d_1	35.631	1.920
d_2	−6.485	40.950
d_3	19.999	41.233

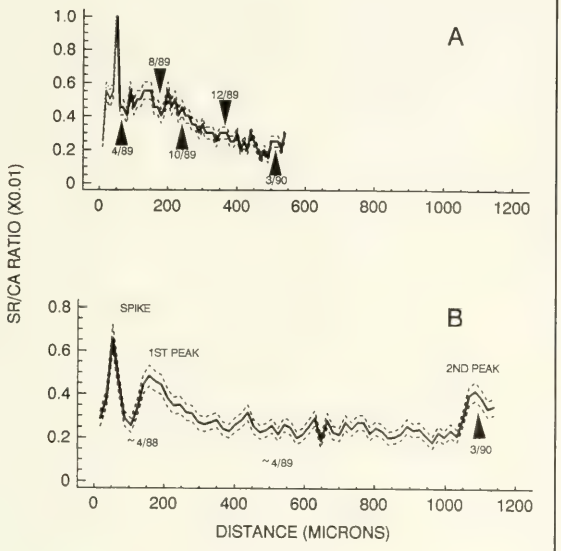

Figure 20

Relationship between Sr/Ca ratios and distance from central primordium towards edge in Dover sole, *Microstomus pacificus*, otoliths. Distances are not comparable between otoliths because transects were not oriented identically. Approximate dates are indicated, based on counts of increments between microprobe marks and the otolith edge. Dashed lines represent 2-σ measurement error, calculated as in Toole and Nielsen (1992). (**A**) 65.7-mm Stage-4 larva collected on 17 March 1990. (**B**) 88.6-mm Stage-5 juvenile collected on 17 March 1990. This fish had one annulus forming at the otolith edge, corresponding to the second Sr/Ca peak.

associated with a habitat transition from warm surface waters to colder midwater depths during the larval to juvenile transition. Dover sole could experience a similar temperature change at the time of AP formation, as discussed below.

Because growth from the central primordium was enclosed by growth from AP in otoliths of most Stage-3 larvae and because new AP were never observed distal to the point of enclosure, the last AP generally formed during either Stage 2 or Stage 3. The presence of very recently formed AP (<7 days) in some Stage-3 larvae and the possibility that additional AP could form in 22% (benthic) to 29% (pelagic) of unenclosed Stage-3 larval otoliths suggest that formation of the last accessory primordium may have occurred during Stage 3, rather than during Stage 2, in some individuals. Because Stage-3 larvae with unenclosed otoliths had lower SINT/BD1A ratios than Stage-3 larvae with enclosed otoliths, it appears that when the last AP does not form during Stage 2, it forms early in Stage 3. Thus, completion of AP formation may occur during the final stages of eye migration, when Dover sole larvae are still pelagic, or after completion of eye migration, shortly after Dover sole first settle to the bottom. In virtually all cases, it occurs before the intestinal loop begins to extend into the secondary body cavity.

Occasional formation of the last AP after settlement in Dover sole corresponds to observations of AP formation in other species. Alhossaini et al. (1989) described unenclosed otoliths of benthic plaice larvae, suggesting that AP formation may not be complete at settlement in that species. Karakiri et al. (1989) noted that the formation of accessory primordia "accompanies" the transition to a bottom-dwelling mode in plaice. If the formation of AP in California halibut "after metamorphosis" (Kramer, 1991) means "after eye migration is complete," then AP formation likely continues after settlement, because settling behavior of California halibut begins prior to initiation of eye migration (Gadomski et al., 1992).

Increased prominence of stress checks following enclosure may have been caused by a change in the otolith growth plane relative to the sectioning plane or by increased intensity of environmental cues that may induce check formation. Campana (1984b) correlated 15-day cycles of increment width and contrast in otoliths of intertidal starry flounder with similar cycles of tidally-induced temperature variation. Rosenberg (1982) described 14-day cycles of check formation in English sole (*Parophrys vetulus*), which first formed "at the beginning of the metamorphic period." An examination of Figure 2 of Rosenberg (1982) suggests that these checks were most obvious proximal to accessory primordia, as in Dover sole. The mean 15.3-day cycle of check formation observed in Dover sole may also be related to tidally induced temperature variation and larvae may be more strongly affected by these patterns following settlement, resulting in more prominent checks distal to the point of enclosure. However, the complex nature of rotational tidal currents in the vicinity of Dover sole nursery grounds precludes an evaluation of this hypothesis at present.

After accessory primordium formation, enclosure of growth from the central primordium, and formation of prominent checks, subsequent changes in larval otolith morphology were continuous, rather than discrete.

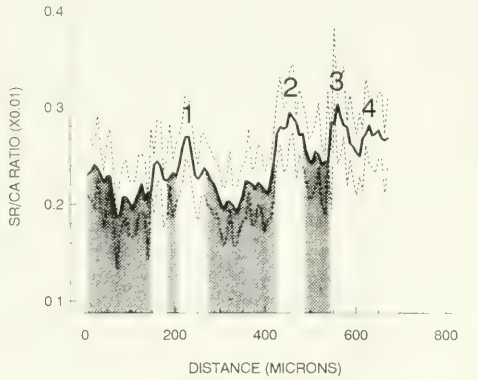

Figure 21

Relationship between Sr/Ca ratios and distance from boundary of enclosure towards edge in a 172.2-mm juvenile Dover sole, *Microstomus pacificus*, collected on 11 September 1989. The specimen had four post-settlement annuli and was prepared in transverse section. Solid line represents five-term running averages of Sr/Ca; dashed lines represent 2-σ measurement error, calculated as in Toole and Nielsen (1992); shaded areas represent opaque zones and unshaded areas represent translucent zones in the otoliths; and numbers above peaks represent post-settlement annuli.

There were no dramatic changes in otolith structure to mark the transition from Stage 3 to Stage 4.

Postmetamorphic juveniles Formation of the first post-settlement annulus occurred during the fall, several months after the transition from larval Stage 4 to juvenile Stage 5 that defines the end of metamorphosis (Markle et al., 1992). While the first and subsequent post-settlement annuli are useful for establishing the number of years since an individual settled and completed metamorphosis, they are not useful for determining either duration of the metamorphic period or the date associated with the end of metamorphosis. No other significant structural landmarks were associated with this stage.

Relation of otolith microchemistry to metamorphic stages

Premetamorphic larvae Within the clear central area formed during Stage 1, Dover sole otoliths exhibited high Sr/Ca levels relative to levels in adjacent opaque areas. Translucent zones of otoliths are rich in aragonite and have a poorly developed protein matrix, while opaque areas have higher protein concentrations (Dannevig, 1955; Williams and Bedford, 1974; Morales-Nin, 1987). Because organics are oxidized during beam exposure and 1:1 concentrations of CO_2 relative to cations are assumed in microprobe calculations (Toole and Nielsen, 1992), differences in concentration of organic materials could differentially affect accuracy of Ca and Sr measurements in translucent and opaque areas. However, Sr and Ca do not fractionate from one another in response to beam damage, so Sr/Ca ratios should not be affected by concentration of organics (Toole and Nielsen, 1992). Protein-poor areas of otoliths are generally associated with rapid growth (Dannevig, 1955; Williams and Bedford, 1974; Morales-Nin, 1987). However, many northeastern Pacific fishes, including adult Dover sole, form translucent zones (annuli) on otoliths during slow winter growth periods (Chilton and Beamish, 1982).

Sr/Ca ratios reflect the substitution of Sr for Ca in otolith aragonite, possibly owing to reduced ability to physiologically discriminate between Sr and Ca during biological precipitation (Radtke et al., 1990). The effect appears to be mediated through Sr concentration in the saccular endolymph, which in turn may be related to plasma protein levels (Kalish, 1989). Sr/Ca ratios have been described as inversely proportional to environmental temperature (Radtke, 1984, 1989; Townsend et al., 1989; Radtke et al., 1990) and growth rate (Sadovy and Severin, 1992), and directly proportional to age (Kalish, 1989), "stress" (Townsend et al., 1989), Sr concentration in ambient water (Kalish, 1990), and salinity of ambient water (Radtke et al., 1988). The latter two effects have only been documented under extreme conditions of seawater vs. freshwater residence. The effects of age described by Kalish (1989) were linked primarily to adults and may not apply to larvae and juveniles in this study.

Elevated Sr/Ca ratios in premetamorphic Dover sole otoliths could be related to a combination of low temperature, slow growth rate, and high "stress" (all of which may be expected to covary) if correlations observed in other studies apply to this species. However, confirmation of these effects in Stage-1 Dover sole is impractical, given available information. Temperatures experienced by premetamorphic larvae depend upon their distance offshore and depth, both of which are variable during this stage (Pearcy et al., 1977; Markle et al., 1992). Because periodicity of increment formation prior to AP formation has not been validated, growth rate cannot be determined with certainty. While it is possible that "stress" may be associated with developmental changes, the strong Sr/Ca spike approximately 48 μm from the central primordium appeared to occur subsequent to events such as hatching (at a length of ≈6 mm; Ahlstrom and Moser, 1975) and initiation of eye migration, caudal fin flexion, and growth

in body depth (at lengths of ≈10–15 mm; Pearcy et al., 1977; Markle et al., 1992), based on radii of otoliths from larvae of known lengths. (The radius of a 17-mm Dover sole larval otolith[2] was 38 µm and otolith radii of 20.6 and 30.1-mm larvae collected in the present study were 75 and 50 µm, respectively [Table 3].) Elevated Sr/Ca levels in the outer portion of the clear central area appeared to form near the termination of Stage 1, when larval morphology does not change (Markle et al., 1992).

Metamorphic larvae during Stage 2 and early Stage 3 Sr/Ca ratios declined in opaque otolith material presumably deposited during Stage 2 and early Stage 3. The decline either levelled prior to formation of the last AP or reached a minimum after enclosure of growth from the central primordium (Fig. 20A). Dover sole probably experienced progressively colder temperatures during this period as they moved from offshore waters onto the continental shelf and from the water column to the bottom (Pearcy et al., 1977; Landry et al., 1989; Markle et al., 1992). However, some larvae continue to move between the bottom and the water column, perhaps on a diel basis, throughout the metamorphic period (Markle et al., 1992), which would add further complexity to this pattern. Larvae appeared to lose mass and either did not grow in length or grew very little during this period (Markle et al., 1992). There was, however, a rapid increase in growth of otoliths, as evidenced by formation of accessory primordia with wide growth increments.

As with Sr/Ca ratios in otoliths of Stage-1 larvae, underlying causes of the observed pattern are unclear. If Sr/Ca ratios in Dover sole responded as in other species, decreasing temperature and slow somatic growth rate would be associated with increasing, rather than decreasing, Sr/Ca ratios. Otolith growth rate may be a better predictor of Sr/Ca ratio than somatic growth rate, and this may become apparent only when the two are uncoupled, as appears to occur during Stage 2 (Fig. 19).

Metamorphic larvae during Stages 3 and 4 Sr/Ca ratios remained low from formation of the last accessory primordium to formation of the first post-settlement annulus (Fig. 20B). Opaque otolith material formed during Stages 3 and 4, when most Dover sole were primarily, if not exclusively, on the bottom (Markle et al., 1992). Dover sole larvae increased in length and weight (Toole and Markle, unpubl. observations) and otolith length increased (Fig. 19) during this time, while bottom temperature decreased and nutrient levels increased following the onset of upwelling (Huyer et al., 1979; Landry et al., 1989). The correlation of low Sr/Ca ratios with rapid growth corresponds to observations of Sadovy and Severin (1992); the correlation of low Sr/Ca ratios with low temperature is contrary to observations of Radtke (1984, 1989), Townsend et al. (1989), and Radtke et al. (1990). Sadovy and Severin (1992) suggest that temperature was not the causative factor of Sr/Ca levels in previous studies; rather, it was an indicator of growth rate, which was positively correlated with temperature. For species such as Dover sole, which reside in upwelling systems where fastest growth occurs at cold temperatures, growth rate appears to over-ride temperature as a predictor of Sr/Ca ratios.

Postmetamorphic juveniles Microchemistry of otolith material deposited during Stage 5, prior to formation of the first post-settlement annulus, was identical to that formed following enclosure during Stages 3 and 4. The first and subsequent annuli were composed of translucent material deposited during the late fall and winter, with a high Sr/Ca ratio. During this period downwelling occurs, resulting in higher water temperature and lower nutrient concentrations than during the spring-summer upwelling season (Huyer et al., 1979; Landry et al., 1989). Kreuz et al. (1982) examined scales of adult Dover sole and noted that fastest growth occurred during the cold upwelling season, rather than during the warmer downwelling season, presumably because of higher productivity. The correlation of high Sr/Ca ratios and slow growth rate during formation of the first and subsequent post-settlement annuli is in agreement with observations of Sadovy and Severin (1992), as is the continued deposition of low Sr/Ca opaque material during subsequent seasons of rapid growth.

Summary of otolith landmarks

Several structural and chemical landmarks were correlated with metamorphic stages of Dover sole (Table 6). These landmarks were highly consistent among otoliths and, when coupled with information from daily growth increments, may be useful in determining timing of developmental and behavioral events associated with metamorphosis.

We conclude that the most consistent landmarks associated with the initiation event of metamorphosis (Markle et al., 1992), which includes movement of the left eye beyond the mid-dorsal ridge, are the transition from clear to opaque otolith material and formation of the first accessory primordium. Completion of eye migration apparently occurs between formation of the first and last AP, which encompasses a period of at

[2]J. Butler, S.W. Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, CA 92038, pers. commun. 1992.

Table 6

Summary of larval and juvenile Dover sole, *Microstomus pacificus*, metamorphic stages (as described in text and Markle et al., 1992), structural landmarks on otoliths, chemical landmarks on otoliths, and habitat.

Stage	Structural landmarks	Chemical landmarks	Habitat
1	Translucent; all growth emanates from central primordium	Sr/Ca ratio high: 0.007–0.010 Spike and 0.004–0.006 "peak"	Pelagic; offshore from continental shelf
2	Opaque material; accessory primordia begin to form	Sr/Ca ratio declines from 0.004–0.006 to 0.002–0.003	Pelagic; moving inshore and towards bottom
End of 2 or beginning of 3	Opaque material; last accessory primordium forms; growth from accessory primordia encloses growth from central primordium	Sr/Ca ratio low, sometimes reaching minimum (=0.002) near point of enclosure	First found on bottom; broad depth distribution on shelf and slope; also caught in midwater
3, 4, 5 Prior to first fall/winter on bottom	Opaque material; checks and left-right asymmetry become more prominent; rostrum forms	Sr/Ca ratio low (0.002–0.003)	Primarily benthic; narrow depth distribution on shelf; some Stage-3 and Stage-4 larvae also caught in midwater
5 Subsequent to first spring/summer on	Translucent material forming during fall/winter; opaque material forming during spring/summer	Sr/Ca ratio high (0.004–0.005) during fall/winter; low (0.002–0.003) during spring/summer	benthic

least 70 days in some individuals. The termination event of metamorphosis, as defined by Markle et al. (1992), is not associated with discrete structural or chemical signals.

We propose that the landmark most likely to correspond with the behavioral change of settlement from water column to benthos is enclosure of growth from the central primordium by growth from accessory primordia. In some individuals a minimal Sr/Ca value near 0.002 may also signal this event. This behavioral change is not instantaneous, because both Stage-3 and Stage-4 larvae were collected in midwater trawls. Markle et al. (1992) characterized settlement in Dover sole as a gradual process in which larvae make their way from an initial deep-water landing zone to a shallower nursery area. Enclosure of growth from the central primordium occurs near the beginning of Stage 3, when Dover sole larvae are first collected on the bottom in significant numbers. Thus, it is reasonable to expect that this is the point at which they first begin to spend a significant amount of time on the bottom.

Chronology of metamorphosis

Periodicity of increments emanating from the central primordium has not been validated, so assignment of dates to otolith landmarks formed during Stage 1 and Stage 2 can only be speculative. However, if increments are deposited approximately daily, then Stage-1 larvae reached a length of 20–30 mm in approximately 2–3 months, some Stage-1 larvae reached 46–50 mm in approximately 5–8 months, and most larvae reached the end of Stage 2 or beginning of Stage 3 about a year after increments first formed. These rates are approximately double those determined from seasonal collections of Dover sole larvae (Markle et al., 1992). Resolution of this discrepency must await validation of increment periodicity in premetamorphic larval otoliths.

Periodicity of growth increments was confirmed for Stage-3 and Stage-4 larvae and Stage-5 juveniles. In general, duration of these stages is in agreement with other studies. The duration of Stage 3 following enclosure averaged 28 days, although it extended at least 65 days for one individual. Because enclosure may oc-

cur during Stage 3, it is possible that total duration of Stage 3 is longer. Markle et al. (1992) suggested that, based on seasonal collections of Stage-3 and Stage-4 larvae, Stage 3 lasted approximately 45 days. Without a landmark for the Stage 3 to 4 transition, duration of Stage 4 could not be determined in this study. However, the combined period of Stages 3 and 4 could last up to 126 days, based on increments distal to enclosure of otoliths from Stage-4 larvae. Markle et al. (1992) observed one captive larva that took 43 days to progress through Stage 4, suggesting a combined duration through Stages 3 and 4 of about 90 days.

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Appendix

Origin of specimens examined for microstructure and microchemistry.

Stage	Number	Date(s)	Collection
1	1	January 1987	Midwater trawl; 300 km off Oregon; upper 200 m of water column
	2	March 1990	Midwater trawl; 75 and 532m bottom depth; upper 30 m of water column (Whipple, 1991[1])
	2	July 1991	Shrimp trawl; off Washington; 128 m depth
	1	October 1991	Shrimp trawl; off Oregon; ≈128 m depth
	Total: 6		
3	89	January 1989, March 1989, January 1990	Shrimp trawl with 6.4-mm liner; off Oregon; 55–377 m (Markle et al., 1992)
	14	March 1990	Midwater trawl; off northern California; bottom depths 73–1462 m; upper 110 m of water column (Whipple, 1991[1])
	Total: 103		
4	66	January 1989, March 1989, January 1990	Shrimp trawl with 6.4-mm liner; off Oregon; 40–170 m (Markle et al., 1992)
	16	March 1990	Midwater trawl; off northern California; bottom depths 33–91 m; upper 30 m of water column (Whipple, 1991[1])
	Total: 82		
5	220	January 1989, March 1989, January 1990	Shrimp trawl with 6.4-mm liner; off Oregon; 75–188 m (Markle et al., 1992)

Geographic variation and sexual dimorphism in the skull of the dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828)

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Abstract.—Variation in skulls of 415 dusky dolphins, *Lagenorhynchus obscurus*, was studied based on 37 standard cranial measurements and meristic variables and 28 nonmetrical characters (NMC) by using both bivariate and multivariate analyses. Geographic variation was analysed in mature skulls from central Peru (N=189), Chile (N=22), New Zealand (N=47) and southwestern Africa (N=40). Advanced fusion in the frontal-supraoccipital suture is the most reliable (95% efficiency) cranial criterion of sexual maturity; distal fusion in premaxillary and maxillary cannot be used. Sexual dimorphism, verified with t-tests and analysis of covariance, was encountered in only 6 of 37 measurements and in none of the NMC characters. Although skull size is the same, males have a wider rostrum and a longer temporal fossa than females. Analyses of covariance and t-tests indicated highly significant differences between geographic groups. A discriminant analysis successfully classified 96.5%, 91.7%, and 90.9% of skulls from respectively the Southeast Pacific (Peru and Chile pooled), New Zealand, and SW Africa. Such differentiation is considered of subspecific level. All methods indicated higher morphological similarity within the Peru/Chile and SW Africa/New Zealand grouped pairs than between the pairs. Most strikingly, skulls from New Zealand and SW Africa are on average 3.1 cm (8.5%) shorter than these from Peru and Chile, concordant with differences in body length. New Zealand specimens differ from SW African animals by smaller tooth size and a greater number of teeth. Nine cranial variables revealed significant variation between dusky dolphins from central Peru and northern Chile, but the degree of heterogeneity should be re-evaluated with a larger sample from Chile. NMC characters confirmed the trends mentioned but resolving power was limited; their use is not recommended as the principal method for subspecific discrimination. The Peruvian dusky dolphin is thought to represent the most ancestral (plesiomorph) form from which the others were derived through dispersion via the east-flowing Westwind Drift.

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The dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828), is mainly encountered in temperate coastal waters off Peru, Chile, Argentina, New Zealand, and South Africa (Gaskin, 1968; Webber, 1987; Van Waerebeek, 1992, a and b). Records, either specimens or sightings, are also available from Namibia[1] (Rose and Payne, 1991) and Angola[2].

This species was originally suggested to have a continuous circumpolar distribution (Brownell, 1965; Hershkovitz, 1966; Mörzer Bruyns, 1971); however, owing to its coast-dwelling habits many authors favor the notion of a disjunct distribution and existence of several isolated stocks (Brownell, 1974; Anonymous, 1975; Leatherwood and Reeves, 1983; Webber, 1987; Webber and Leatherwood, 1990). Nevertheless, evidence to support this hypothesis is lacking. Possible pelagic occurrence of dusky dolphins in the southern oceans and off many oceanic islands remains unknown. Specimen records are documented from the Campbell, Auckland, and Chatham Islands around New Zealand (Gaskin, 1968; Baker, 1983; Webber, 1987), the Falkland Islands (British Museum of Natural History specimens; Brownell, 1965) and from Gough Island (40°20'S, 10°00'W) on the mid-Atlantic Ridge[3]. Presence of dusky dolphins off southern Australia and Tasmania (reviewed by Webber, 1987; Van Waerebeek, 1993) and off the Kerguelen Islands (Robineau, 1991) could not be confirmed. Kasamatsu et al.[4] reported a single sighting from south of Madagascar but no photographs were taken and both the unusual (for *L. obscurus*) sea surface temperature (25°C) and offshore location solicits some caution. The sighting of a group of *Lagenorhynchus* sp. in deep tropical waters of the South Pacific, for instance, resulted in considerable debate before they were identified as *L. australis*, despite the availability of excellent photographs (Leatherwood et al., 1991).

Incidental fishing mortality occurs throughout the range of dusky dolphin and it is heavily exploited in Peru (Read et al., 1988; Van Waerebeek and Reyes, 1990, 1993) and, locally, off northern Chile (Van Waerebeek and

[1]P.B. Best, South African Museum, pers. commun. February 1991.

[2]P.B. Best, South African Museum, unpubl. photograph, identification confirmed by author.

[3]P.B. Best, South African Museum, unpubl. photographs, identification confirmed by the author.

[4]Kasamatsu, F., G. Joyce, P. Ensor, and J. Mermoz. 1990. Current occurrence of Cetacea in the southern hemisphere; results from the IWC/IDCR southern hemisphere minke whale assessment cruises, 1978/79–1987/88. Doc. SC 42/015 presented to the Int. Whal. Comm. Sci. Committee, 77 p.

Guerra, 1986[5]; Guerra et al., 1987). Population identification is needed so that breeding units can be managed separately. Cranial measurements have been used to discriminate populations in several delphinids including the common dolphin, *Delphinus delphis* (Evans, 1975, 1982; Heyning and Perrin[6]), bottlenose dolphin, *Tursiops truncatus* (Ross, 1977; Walker, 1981[7]), tucuxi, *Sotalia fluviatilis* (Borobia and Sergeant, 1989), pantropical spotted dolphin, *Stenella attenuata*, and spinner dolphin, *S. longirostris* (Perrin, 1975, a and b; Perrin et al., 1979; Schnell et al., 1982[8], 1985; Douglas et al., 1984).

In addition to skull measurements, non-metrical cranial characters have also been employed in population studies: harbor porpoises, *Phocoena phocoena* (Sjovold, 1977; Kinze, 1985, 1990[9]), spotted and spinner dolphins (Perrin et al., 1982[10]; Yablokov et al., 1983) and common dolphins (Perrin et al., 1988[11], 1989). The resolving power of non-metrical methods has been difficult to assess, however, because the identities of the dolphin stocks on which the technique was applied were debatable and results somewhat equivocal (Perrin et al., 1988[11], 1989). Also, non-metrical methods are more prone to observer bias and drift in character-state evaluation over time, especially if large samples are involved (e.g., Perrin et al., 1982[10], 1989).

Of the six extant species of *Lagenorhynchus*, geographic variation has been examined for the three northern hemisphere species: Pacific white-sided dolphin, *L. obliquidens* (Walker et al., 1986), Atlantic white-sided dolphin, *L. acutus*, and whitebeaked dolphin, *L. albirostris* (Mikkelsen, 1991). The purpose of this paper is to quantify sexual dimorphism and individual and geographical variation in skulls of *L. obscurus* from Peru, Chile, southwestern Africa (including South Africa, Namibia and Angola), and New Zealand utilizing material currently available in scientific collections. Evidence for separate dusky dolphin populations, as presented below, should urge agencies responsible for marine resource management in aforementioned coastal states to take special steps to ensure the conservation of *L. obscurus* on a stock by stock basis, rather than to evaluate the status of the species on a global scale.

Material and methods

Skulls were obtained by the author from animals recently killed in fishery operations as well as from museum specimens with widely variable degrees of documentation. Of more than 300 cranial specimens of *L. obscurus* from central Peru, collected along a coastal strip between Huacho (11°10'S) and San Andrés (13°50'S) in the period 1984 to 1990, 239 skulls were adequate for study. The majority of these were obtained from freshly butchered dusky dolphins at the wharves of Pucusana (12°30'S) and Cerro Azul (13°00'S); the rest were retrieved from decomposed remains at local fish-offal dumps or were beach-cast. When available, biological data, including sex, standard body length (SL) and reproductive status, were recorded for each specimen. Skulls were deposited at the Centro Peruano de Estudios Cetológicos, Pucusana, Peru; the Zoölogisch Museum of the University of Amsterdam; the Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussels); and at the U.S. National Museum of Natural History, Washington D.C. Surveys to collect stranded and by-caught specimens in northern Chile were carried out in collaboration with colleagues from the Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, Antofagasta, Chile (Van Waerebeek and Guerra, 1986[5]; Guerra et al., 1987).

The remainder of cranial material was located at the following institutions: the American Museum of Natural History, New York; British Museum (Natural History), London; Canterbury Museum and Canterbury University, Christchurch, New Zealand;

[5]Van Waerebeek, K. , and C. Guerra. 1986. Review of the distribution and status of the Burmeister's porpoise in Chile. Cetacean survey in II region of Chile, August–September 1986. Instituto de Investigaciones Oceanologicos, Universidad de Antofagasta, casilla 170, Antofagasta, Chile. Unpubl. Rep., 13 p.

[6]Heyning, J. E., and W. F. Perrin. 1991. Re-examination of two forms of common dolphins (genus *Delphinus*) from the eastern North Pacific; evidence for two species. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-28, 37 p.

[7]Walker, W. A. 1981. Geographic variation in morphology and biology of bottlenose dophins (*Tursiops*) in the eastern North Pacific. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin Rep. LJ-81-03C, 54 p.

[8]Schnell, G. D., M. E. Douglas, and D. J. Hough. 1982. Geographic variation in morphology of spotted and spinner dophins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-82-15C, 213 p.

[9]Kinze, C. C. 1990. Non-metric analysis of harbour porpoises (*Phocoena phocoena*) from the North and Baltic seas: implications for stock identity. Unpubl. Paper SC/42/SM35 presented to the IWC Sci. Committee, June 1990.

[10]Perrin, W. F., A. V. Yablokov, and V. L. Cass. 1982. Preliminary report on the use of non-metrical skull characters to discriminate populations of pelagic dophins. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-82-14, 32 p.

[11]Perrin, W. F., A. V. Yablokov, J. Barlow, and M. V. Mina. 1988. The use of non-metrical skull characters for analyzing geographical variation in the common dolphin, *Delphinus delphis*. Part 1: Selection of characters. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-88-20, 24 p.

Departamento de Ciencias del Mar, Universidad Arturo Prat, Iquique, Chile; Museo Nacional de Historia Natural, Santiago de Chile; National Museum of New Zealand, Wellington; Otago Museum and Otago University, Dunedin, New Zealand; Port Elizabeth Museum, Port Elizabeth, and South African Museum, Cape Town, South Africa; U.S. National Museum of Natural History, Washington D.C.; and the Zoölogisch Museum, University of Amsterdam. Unfortunately, only a very few skeletal specimens from the SW Atlantic are available in Argentinian collections[12] and, for reasons of economy, it was impractical to examine these. Metrical and non-metrical data sets were collected by the author only, in order to reduce error and observer bias as a source of variation.

Cranial maturity

Juvenile specimens were excluded from the sample to reduce variability due to age. As many skull specimens did not have sexual maturity data, mature skulls were selected partly by using indirect criteria. To identify one or more cranial indicator(s) of sexual maturity in *L. obscurus*, selected sutures were inspected in 85 skulls (48 females, 37 males) from sexually mature specimens from Peru and in 31 skulls from subadults (large sexually immature specimens) from Peru, SW Africa, and New Zealand. Skulls which had been boiled (moderate heating for maceration excepted) or chemically treated were not included.

The degree of suture fusion between cranial elements was scored as: 0= no fusion, elements can be moved freely; 1= limited fusion, suture line clearly visible at all points; or 2= advanced fusion with partial obliteration of suture line. Occlusion of the pulp cavity in teeth (OCCL) was scored as: 0= wide open; 1= partially occluded; or 2= occlusion complete. The following seven cranial sutures were defined as follows:

SYM	symphysis mandibularis (between left and right ramus)
MXDIST	distal maxilla-premaxilla suture (rostral distal fusion)
PTPAL	pterygoid-palatine suture
PTBAS	pterygoid-basioccipital suture
LAC	lacrimal-maxilla/frontale suture
ZYG	zygomatic-parietal/exoccipital suture
FROC	frontal-supraoccipital suture.

The selection criteria for adult skulls were, in decreasing order of priority:

1 Skulls of sexual mature specimens as evidenced in males by presence of seminal fluid upon gross examination of the epididymis (Sergeant, 1962); in females by presence of at least one corpus luteum or corpus albicans in the ovaries or if lactating or pregnant, or both;

2 Advanced fusion (score 2) in the frontal-supraoccipital suture or advanced fusion in at least two of the other six defined cranial sutures.

The complete fusion of thoracic vertebral epiphyses, indicating physical maturity, was used to confirm cranial maturity of some specimens.

Metrical characters

Thirty-three standard metrical variables measured with vernier calipers to the nearest mm and four tooth counts, adapted from Perrin (1975a) and Schnell et al. (1982[8]) (see Table 3) were recorded for 381 dusky dolphin skulls. Standardized skewness and kurtosis were computed for all sample variables; if significant departure from normality was suspected, a Kolmogorov-Smirnov (K/S) one-sample test of the fit was applied. A ratio of variances test with 95% confidence limits was used to verify homogeneity of variance in all sample pairs. STATGRAPHICS version 4.2 programme (STSC Inc., 1989) was used on an AT286 personal computer for most statistical applications. The α=0.05 level was the criterion chosen for significance. All t-tests were two-sided. Owing to the large series of t-tests, a few significant results (false positives) should be expected to occur by chance alone.

Sexual dimorphism in cranial measurements and tooth counts was studied by means of t-tests and analysis of covariance (ANCOVA, with condylobasal length as covariate) in skulls of sexually mature females (N=59) and males (N=50) from central Peru. To permit pooling of sexes and utilization of cranially mature skulls of unknown sex, the few sexually dimorphic characters were not further considered in the analysis of geographic variation.

Seasonal variation was examined for in all variables by using a multifactor analysis of covariance (MANCOVA) with three-monthly seasons (January–March, April–June, etc.) and sex as classification variables.

Geographic variation was analysed for skulls from Peru (59 females, 50 males and 80 of unknown sex), New Zealand (N=47), SW Africa (N=40) and Chile (N=22). Both a one-way analysis of variance (ANOVA) and an ANCOVA with skull CBL as covariate and with geographic region as classification variable were utilized to assess among-group variation in skull size and shape. Next, most morphologically similar group pairs,

[12] R. N. P. Goodall, Centro Austral de Investigaciones Cientificas, Ushuaia. Pers. commun. July 1988.

namely Peru/Chile and SW Africa/New Zealand were compared by means of *t*-tests to identify discriminating variables.

Discriminant analyses (DISCRIM) were performed on samples limited to specimens with a complete set of measurements. This sample included 135 skulls from Peru, 24 from New Zealand, 22 from SW Africa and 7 from Chile. A first DISCRIM with 21 characters maximized discrimination between geographic groups. Subsequently, a series of discriminant analyses was executed by considering various combinations of a small number of highly variable cranial characters so that an optimum segregation between groups was obtained. These discriminant functions can be used tentatively to assign undocumented museum skulls to respective populations. It must be cautioned however that no specimens from Argentina have been examined and the discriminant locus of that population remains unknown.

Non-metrical characters

Initially, 35 non-metrical cranial characters (NMC), following Perrin et al. (1982[10]), were determined, but serious problems with score repeatability over time reduced the number of usable NMC to 27 (Table 1 and Fig. 1). Similar problems have been reported for the common dolphin by Perrin et al. (1988[11], 1989).

Analysis of sexual dimorphism was limited to skulls of sexually mature specimens from central Peru (N=109), eliminating influences of growth and geography. Sexually monomorphic characters (the full set, see Results) were then tested for dependence on cranial maturity status in 173 mature and 48 immature skulls. Geographic variation in non-metrical traits among the four geographic areas was studied after eliminating variables influenced by sex and maturity. All significance testing of variation in NMC was done by means of chi-square contingency analyses. Tooth counts were compared by *t*-tests.

Table 1

Non-metrical cranial characters utilized in present study (from Perrin et al., 1982[6]); see Figure 1.

Character 1L/1R (left/right).	Position of the foramen (A in Figure 1) in the premaxillary at the base of the prenarial triangle, relative to the level of the anteriormost projection of the antorbital processes. Codes: 1=at; 2=ahead; 3=behind the level.
Character 2L/2R.	Position of the anteriormost large foramina (B) in the maxillary relative to the level of the anteriormost projection of the antorbital processes. Codes: 1=at; 2=ahead; 3=behind the level.
Character 3.	Asymmetry of position of the two anteriormost large maxillary foramina (B). Codes: 1=symmetrical; 2=left foramen more anteriorly placed; 3=right foramen more anterior.
Character 5L/5R.	Number of small foramina (C) in the maxillary anterior to the anteriormost of the large foramina. Codes: 1=one foramen; 2=two foramina;3 etc.; 6=no foramina.
Character 6L/6R.	Number of foramina (D) in the maxillary behind a line at the level of the anterior edge of the external nares and perpendicular to the long axis of the skull. Codes: 1=1 foramen; 2=2 foramina; 3 etc.; 6= no foramina.
Character 9L/9R.	Contact between maxillary and occipital, at point where occipital crest intersects margin of temporal fossa (E). Codes: 1=contact (or space of <1mm); 2=no contact.
Character 10.	Contact between premaxillary and nasal, on right side (F). Codes: 1=contact (or space of <1mm); 2=no contact.
Character 12L/12R.	Presence of an antorbital notch (G). Codes: 1=notch present; 2=not present.
Character 13.	Composition of the antorbital process, in lateral view, on left side (H). Codes: 1=formed by lacrimal; 2=formed by lacrimal and frontal; 3=formed by lacrimal and maxillary.
Character 16.	Accessory foramen above foramen magnum (I). Codes: 1=present; 2=absent.
Character 17.	Clear notch in upper margin of foramen magnum (J). Codes: 1=present; 2=absent.
Character 18L/18R.	Fenestrations in occipitals, near foramen magnum and in exoccipital region (K). Codes: 1=one fenestration; 2=two; 3 etc.; 6=no fenestrations.
Character 19.	Fenestrations in region of occipital swellings (L). Codes: 1=one fenestration; 2=two etc.; 6= no fenestration.
Character 23.	Posterior contact between pterygoid hamuli (M). Codes: 1=open (gap >1mm); 2=closed.
Character 24.	Anterior contact between hamuli (N). Codes: 1=open (gap>1mm); 2=closed.
Character 25.	Spine of palatines visible in anterior gap between hamuli (O). Codes: 1=visible; 2= not visible.
Character 30.	Mesial fenestration in basisphenoid (R). Codes: 1=foramen present; 2=absent.
Character 33L/33R.	Number of mental foramina. Codes: 1=1; 2=2; etc.
Character 34L/34R.	Arrangement of mental foramina. Codes: 1=foramina lie along a simple curve; 2=foramina do not lie along a simple curve.

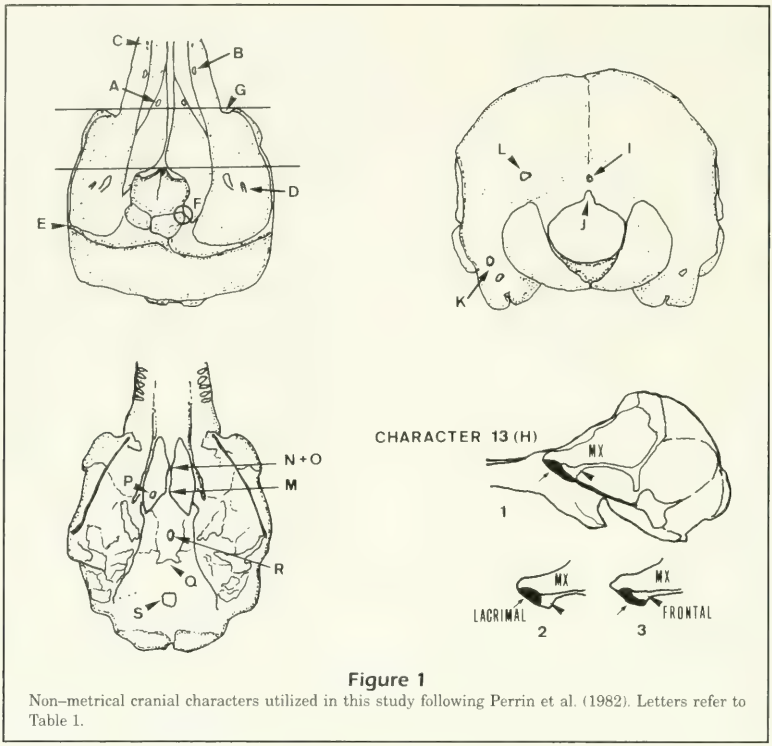

Figure 1

Non–metrical cranial characters utilized in this study following Perrin et al. (1982). Letters refer to Table 1.

Results

Cranial maturity

Relationships between the degree of fusion in cranial sutures and sexual maturity for *L. obscurus* are shown in Table 2. Less than 25% of the adults exhibited advanced rostral distal fusion (MXDIST=2) which, as in *L. obliquidens* (see Walker et al., 1986), eliminates MXDIST as a selection criterion for adult skulls in this species (too many useful skulls would be rejected). However, three other sutures, frontale-supraoccipitale (FROC), zygomatico-parietale/exoccipitale (ZYG), and lacrimale-maxilla/frontale (LAC), had advanced fusion (state=2) in 95%, 89%, and 85%, respectively of the sexually mature specimens. Equally important, only two sexually immature specimens from New Zealand showed full fusion in any of these sutures: one was a pubescent female with large follicles (ZM39957) and the other, an unusually large female without ovarian corpora (ZM39561, 187 cm). Moreover, based on overall size, those skulls fitted into the adult series. Skulls with at least some fusion (state 1 or 2) in either MXDIST, SYM, or PTPAL are very likely from sexually mature dolphins (see Table 2).

Metrical characters

Individual variation Summary statistics for cranial characters in adult female and male dusky dolphins of central Peru are presented in Table 3. Of 74 characters tested, only one (upper left tooth count, for females) departed significantly from normality (Kolmogorov-Smirnov, P=0.017), which could be attributed to chance fluctuations. Homogeneity of variance (95% confidence, TWOSAM, STSC Inc., 1989) was confirmed for all sex-paired characters.

Statistics summarizing individual variation in cranial characters are given also for mature dusky dolphins of northern Chile, southwestern Africa and New Zealand (Table 3). No significant departures from nor-

Table 2

Percent frequencies, rounded to nearest integer, for degrees of fusion seen in cranial sutures of *Lagenorhynchus obscurus* specimens of known sexual maturity status (sexes pooled). Mature animals are all from Peruvian waters; subadults include specimens from Peru, southwestern Africa, and New Zealand. States of fusion are: 0= unfused; 1= some fusion; 2= advanced fusion. Cranial sutures are defined in text.

Suture	Subadults (%) Fusion state				Mature (%) Fusion state			
	N	0	1	2	*N*	0	1	2
SYM	31	94	3	3	71	47	28	25
MXDIST	29	100	0	0	77	23	53	23
PTPAL	30	97	3	0	85	4	28	68
PTBAS	30	80	20	0	85	4	28	68
LAC	30	50	50	0	85	0	15	85
ZYG	31	81	13	6	85	1	9	89
FROC	31	45	48	6	85	0	5	95
OCCL	—	—	—	—	90	4	41	54

mality were encountered in any of the characters (K/S, $P>0.5$).

Sexual dimorphism The overall size of the adult dusky dolphin skull, based on condylobasal length and zygomatic width, is equal in males and females (t-tests, $P>0.50$; Tables 3 and 4). Highly significant sexual dimorphism (t-tests, $P<0.005$) was found in the width of the rostrum over most of its length (RW60, RW1/4, RW1/2, PMX1/2, RW3/4) and in the length of the temporal fossa; males had consistently higher mean widths. Analyses of covariance showed sexual dimorphism in exactly the same variables and with very similar significance levels as in the two-sided t-tests, indicating proportional differences (shape). However, it is uncertain whether the observed, small dissimilarities have biological meaning, particularly as there is wide overlap in ranges. I was unable to produce a satisfactory model to predict the sex of an unknown animal through stepwise variable selection in a multiple regression (see Douglas et al., 1986) exactly because of those subtle deviations.

Twenty-four of 36 characters showed significant correlations with the condylobased length (CBL) covariate, including five of the six dimorphic characters (Table 4), implying that much of the variability is explained by variation in CBL. Eliminating dimorphic characters from the geographic analysis therefore entails little loss of information.

Seasonal variation An analysis of seasonal variation was feasible only for Peruvian specimens. Skull size (CBL) was not seasonally dependent (MANCOVA, $F=1.45$, df=3, $P=0.23$) but six other skull characters (RW60, RW1/4, APL, RAL, TCUL, and TCUR) demonstrated seasonal variation at a low level of significance (MANCOVA, $0.05 < P < 0.02$). However, at least in the case of RW60, RW1/4, and RAL, significant interactions due to sexual dimorphism in these measurements seemed to be the cause (P-values for 2-factor interactions were respectively 0.039, 0.047, and 0.037). In APL, TCUL, and TCUR, which are sexually monomorphic characters (see above), there were no sex/season interactions ($P>0.50$). The significance in these few cases could be due to chance in view of the large number of t-tests. This is supported by the results of a series of Runs tests (Runs above and below median, Runs up and down, STSC Inc., 1989) on chronologically ordered CBL, tooth counts and tooth widths. These results did not suggest any non-randomness ($Z>0.05$ for all tests).

Geographic variation Exclusion of the few sexually dimorphic characters allowed combining samples of males and females and the use of cranially mature skulls of unknown sex. Highly significant differences between geographic regions were confirmed for 29 of 31 cranial characters (for all ANOVA, $P<0.005$ and mostly $P<0.0001$; Table 5). Tympanic bulla width (BW) proved divergent between groups but with less confidence (ANOVA, $F=4.1$, df=3,117, $P=0.019$) and no difference could be detected for periotic length (ANOVA, $F=0.24$, df=3,201, $P=0.87$). Variance generally was homogeneous (Cohran's C-test and Bartlett's test, $P>0.01$ and mostly $P>0.05$); exceptions include TCLL (Cohran's, $P=0.006$) and PEL (Cohran's, $P=0.003$; Bartlett's, $P=0.009$).

ANCOVA analyses revealed discernible variation in 16 of 30 skull characters which can not be attributed to divergences in skull size alone but are due to proportional differences (i.e., shape); 11 characters were highly significantly different between geographic groups ($P<0.01$, Table 5). Means and 95% confidence intervals are plotted for each variable against geographic region (Fig. 2). The most striking element is the overwhelming difference in skull size, reflected in most measurements, grouping skulls from Peru and Chile and specimens from New Zealand and Southwest Africa. Skulls of dusky dolphins from the latter pair-group have, on average, a CBL about 3 cm shorter than skulls from Peru and Chile.

Table 3

Skull measurements (in mm) and tooth counts of mature dusky dolphins *Lagenorhynchus obscurus* from different populations. Sexes are pooled except for Peru; tooth counts of Chilean specimens include some juvenile specimens. Skull selection criteria are explained in text.

Zealand	Peru Females				Peru Males				Chile				SW Africa				N e w			
Variable	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range
Condylobasal length (CBL)	59	398.4	12.6	368–426	49	396.9	11.3	372–420	14	394.9	9.57	377–410	34	365.8	11.0	342–386	41	367.0	10.9	344–388
Rostrum length (RL)	59	221.8	9.19	198–224	49	219.5	8.29	202–241	13	220.8	9.41	208–235	36	198.8	7.0	178–214	42	198.4	9.0	178–215
Rostrum width at base (RWB)	59	101.1	4.63	87–112	50	101.5	4.84	92–113	21	100.5	4.71	89–109	39	97.7	5.4	75–107	45	97.2	4.6	89–108
Rostrum width at 60% (RW60)	59	74.7	3.35	68–82	50	76.9	3.62	68–84	21	74.8	3.47	69–80	40	67.8	3.2	59–75	45	66.7	3.4	61–77
Rostrum width at 75% length (RW75)	58	75.5	3.21	69–83	49	77.8	3.55	69–85	16	76.1	3.36	70–82	36	70.1	2.8	64–76	41	68.6	3.3	63–78
Rostrum width at 1/2 length (RW1/2)	59	65.3	2.95	59–72	49	67.5	3.4	59–75	16	66.3	3.93	58–71	36	60.2	2.9	54–68	42	59.2	3.5	53–67
Premax. width at 1/2 length (PMX1/2)	59	35.5	2.44	29–41	49	37.2	2.68	32–43	16	36.7	2.55	33–41	36	34.1	2.1	30–40	42	32.8	2.5	27–39
Rostrum width at 3/4 length (RW3/4)	59	48.2	2.44	42–54	49	50.3	2.78	45–57	16	49.4	4.45	41–55	33	45.5	3.0	39–53	39	44.9	3.1	39–50
Rostrum tip to ext. nares (RTEN)	58	264.1	11.0	232–228	46	262.2	9.33	245–284	14	259.9	12.8	229–277	35	237.3	8.0	214–250	40	239.8	12.1	198–261
Rostrum tip to int. nares (RTIN)	58	261.5	11.2	232–228	49	260.0	10.8	240–283	10	259.6	8.98	246–274	28	235.1	8.0	219–250	35	238.1	9.2	214–254
Preorbital width (PROW)	57	166.9	4.89	151–117	50	167.6	4.19	159–178	19	164.3	6.0	154–178	32	159	4.7	151–169	43	158.9	5.7	145–171
Postorbital width (POOW)	57	184.4	5.54	168–119	50	184.8	4.97	176–198	16	184.0	5.98	175–195	33	175.4	4.8	164–186	40	175.8	5.4	166–190
Zygomatic width (ZYW)	57	187.6	5.17	178–119	50	188.3	5.59	179–202	17	187.2	5.85	178–199	34	177.8	5.2	165–191	44	177.7	5.4	167–194
Parietal width (PARW)	59	152.6	6.11	137–116	50	153.9	5.96	135–166	15	154.6	6.16	146–166	37	150.8	5.1	136–160	46	150.2	5.5	138–160
Greatest width premax (GWPMX)	59	78.0	2.98	72–85	50	77.3	2.76	72–83	22	78.2	3.16	74–86	40	76.0	3.2	68–85	47	75.9	3.6	67–85
External nares width (ENW)	59	55.4	2.56	48–62	50	54.5	2.31	50–59	22	54.2	2.22	50–59	39	54.4	2.6	47–61	47	53.2	2.6	49–61
Temporal fossa length (TFL)	59	71.4	3.87	62–80	50	74.2	4.9	63–86	13	74.0	3.51	66–79	36	69.6	4.4	59–78	47	69.6	4.0	60–76
Temporal fossa width (TFW)	59	52.4	3.41	43–62	50	52.8	3.98	44–65	16	52.5	3.08	48–57	37	51.1	3.8	41–60	47	49.5	3.0	43–56
Orbit length (ORL)	58	52.2	2.35	48–58	50	52.1	2.32	48–59	18	52.8	2.24	47–56	35	51.0	2.4	45–56	46	49.8	2.1	45–56
Antorbital process length (APL)	58	38.1	2.89	32–45	50	38.7	2.76	33–46	17	36.3	2.11	32–40	37	34.8	2.8	29–41	46	35.5	3.3	26–42
Internal nares width (INW)	59	57.7	3.04	51–65	50	57.7	2.81	52–64	18	56.9	3.07	53–63	37	52.4	2.5	47–57	44	53.7	2.7	48–60
Pterygold length (PTEL)	55	65.5	4.3	57–77	50	64.4	4.0	56–74	11	62.1	2.74	57–66	30	59.0	4.0	51–73	35	57.7	4.0	49–66
Upper tooth row length (UTRL)	59	192.9	8.38	171–221	49	190.1	7.58	171–207	13	191.2	7.25	180–204	32	171.2	6.4	153–182	43	170.2	8.2	151–183
Lower tooth row length (LTRL)	55	192.7	7.54	171–220	47	190.9	8.16	171–210	11	183.5	9.09	172–195	34	172.4	7.5	159–187	41	170.7	8.5	143–191
Ramus length (RAL)	55	335.4	9.97	312–360	47	334.5	11.3	309–360	11	327.9	10.52	311–346	32	308.6	10.1	286–330	40	306.3	9.6	284–326
Ramus height (RAH)	54	69.2	2.95	63–80	47	69.3	2.65	62–74	9	68.8	1.92	66–71	31	65.1	2.6	60–71	40	65.3	2.6	60–71
Tooth count upper left (TCUL)	58	32.0	1.59	29–37	49	31.8	1.73	29–36	17	30.9	2.07	26–34	29	30.4	1.6	28–34	36	31.9	1.8	28–37
Tooth count upper right (TCUR)	58	32.0	1.74	29–39	49	31.8	1.69	29–36	14	30.6	1.9	26–33	30	30.2	1.7	27–33	37	32.0	1.6	29–36
Tooth count lower left (TCLL)	55	31.1	2.06	26–37	47	31.3	1.58	28–36	14	30.2	1.97	28–35	31	29.6	1.5	26–32	40	31.5	2.2	28–39
Tooth count lower right (TCLR)	55	30.8	2.14	26–37	47	31.0	1.41	28–36	17	30.4	2.26	27–35	32	29.6	1.5	27–34	40	31.4	2.2	27–37
Tooth width at mid-jaw (TW)	55	4.4	0.36	3.7–5.1	49	4.4	0.35	3.6–5.5	16	4.3	0.28	3.7–4.7	36	4.18	0.37	3.3–5.2	32	3.65	0.35	2.9–4.3
Maximum bulla length (BL)	55	35.4	1.19	33–39	49	35.4	1.38	33–38	5	34.6	0.89	34–36	30	34.0	1.1	32–36	18	33.9	1.2	31.5–36
Maximum bulla width (BW)	20	19.8	0.69	19–21.5	20	19.7	0.85	18.5–21.5	—	—	—	—	30	19.5	0.6	18.5–20.5	15	19.3	0.7	18–20.5
Height braincase (HBR)	58	109.5	4.45	101–119	50	110.3	4.45	100–119	19	109.9	5.25	103–21	37	107.1	4.0	99–119	45	105.0	4.8	93–115
Length braincase (LBR)	58	126.9	4.6	113–138	50	127.9	4.04	118–134	19	125.9	3.93	117–133	37	122.5	4.3	113–131	45	121.6	4.2	112–131
Periotic length (PEL)	54	30.2	1.16	28–33	49	30.33	1.06	27–32	6	30.5	1.64	28–33	27	30.0	1.2	28–32	12	30.4	1.3	28–32
Height crest (HCR)	52	7.66	2.13	3.9–14.5	48	7.17	1.77	4–12.5	–	–	—	—	30	5.5	2.1	1–10	41	7.2	2.1	3.5–13

Table 4

Results of two-sided *t*-tests and multifactor analysis of covariance (MANCOVA) to determine sexual dimorphism and seasonal variation (see text) in skull measurements of mature female (N=59) and male (N=50) *Lagenorhynchus obscurus* from Peru. Condylobasal length (CBL) is used as the covariate. Measurements are defined in the text.

			MANCOVA			
	Two-sided *t*-test		Covariate (CBL)		Factor 1 (sex)	
Variable	*t*	*P*	*F*-ratio	*P*	*F*-ratio	*P*
CBL	0.63	0.53	—	—	0.37	0.55
RL	1.33	0.19	328	<0.0001	2.0	0.16
RWB	0.49	0.62	0.43	0.52	0.32	0.58
RW60	3.32	<0.002	12.3	<0.001	12.1	<0.001
RW1/4	3.62	<0.0005	4.87	<0.05	12.8	0.0005
RW1/2	3.58	<0.0001	12.3	<0.0001	13.1	0.0005
PMX1/2	3.59	<0.0001	0.29	0.59	10.4	0.002
RW3/4	4.2	<0.0001	8.72	<0.005	18.7	<0.0001
RTEN	0.93	0.36	201.5	<0.0001	0.001	0.98
RTIN	0.74	0.46	470.4	<0.0001	0.29	0.59
PROW	0.78	0.44	13.3	<0.0005	0.71	0.41
POOW	0.31	0.75	12.38	<0.001	0.04	0.84
ZYW	0.64	0.52	16.8	0.0001	0.62	0.44
PARW	1.17	0.24	2.41	.012	1.40	0.24
GWPMX	1.29	0.20	1.68	0.20	1.54	0.22
ENW	1.74	0.09	0.91	0.35	2.98	0.09
TFL	3.36	<0.005	7.35	<0.01	10.54	0.002
TFW	0.61	0.54	0.05	0.94	0.13	0.72
ORL	0.19	0.85	35.1	<0.0001	0.63	0.44
APL	1.26	0.21	2.70	0.10	1.54	0.22
INW	0.10	0.92	3.31	0.07	0.01	0.92
PTEL	1.39	0.17	30.5	<0.0001	1.1	0.30
UTRL	1.75	0.08	281.5	<0.0001	3.56	0.06
LTRL	1.10	0.27	135.1	<0.0001	0.26	0.61
RAL	0.42	0.67	386.2	<0.0001	0.54	0.47
RAH	0.06	0.95	13.4	<0.0005	0.07	0.79
TCUL	0.76	0.45	4.79	<0.05	1.41	0.24
TCUR	0.65	0.51	4.73	<0.05	0.95	0.34
TCLL	0.53	0.60	1.42	0.24	0.08	0.78
TCLR	0.54	0.60	1.32	0.25	0.09	0.77
TW	0.08	0.94	4.63	<0.05	0.36	0.55
BL	0.05	0.96	15.6	0.0002	0.003	0.96
BW	0.41	0.69	0.26	0.62	0.008	0.93
HBR	0.95	0.35	5.14	<0.05	1.72	0.19
LBR	1.20	0.23	42.3	<0.0001	2.55	0.11
PEL	0.64	0.52	29.1	<0.0001	0.84	0.37
HCR	1.26	0.21	2.67	0.11	1.98	0.16

Southwest African versus New Zealand population Results of two-sided *t*-tests comparing adult skulls from southwest Africa and New Zealand are presented in Table 6. Skulls from these regions do not differ in size, as indicated by condylobasal length (t=0.48, P=0.63) and zygomatic width (t=–0.074, P=0.94). Nevertheless, the two populations are strikingly divergent in dentition. Mean tooth width for New Zealand dusky dolphins (3.56 mm, SD=0.35, N=32) is highly significantly smaller (t=–7.14, P<0.0001) than in SW African dusky dolphins (4.18 mm, SD=0.37, N=36); the difference is visually obvious even from a quick inspection of skulls. In addition, New Zealand crania have on average 1.5–1.8 teeth more in each row than African skulls (two-sided *t*-tests, P<0.001). Maximum tooth counts in the four rows range 32–34 (SA) and 36–39 (NZ). Finally, SW African crania have a significantly lower supraoccipital crest (t=3.43, P=0.005), slightly wider external nares and temporal fossa and, possibly, a somewhat higher braincase (0.05<P<0.01) than the New Zealand specimens.

Peruvian versus Chilean population Dusky dolphin crania from central Peru and northern Chile showed no meaningful overall size differences, as indicated by CBL and ZYG (Table 6). The antorbital process (APL) and the lower tooth row (LTRL) however were very significantly shorter (*t*-test, P<0.005) and mean tooth counts were lower in Chilean animals. Small but statistically discernible deviations (P<0.05) were detected also in PROW, PTEL, and RAL. These data suggest that at least some genetic distance exists between *L. obscurus* stocks from central Peru and northern Chile, but it is recommended that the sample size for Chile be increased before definite conclusions be made.

Multivariate analysis Results of the discriminant analyses (DISCRIM) with a maximum of characters (21) fully confirm findings from bivariate techniques (Table 7); scores on first and second axis are shown in Figure 3. The first discriminant function differentiated well between population pairs Peru/Chile and New Zealand/SW Africa; the second function largely separated SW Africa and New Zealand stocks (Fig.4), whereas the third function projected the Chile group at the positive extreme of the z-axis (see group centroids, Table 7). The discriminant functions successfully predicted the actual group most of the time, i.e., from 85.7% of cases in Chile to 91.7% in New Zealand. When Chilean and Peruvian animals were combined into a single "Southeast Pacific stock," 96.5% (137 of 142) of these were correctly allocated. Only two of 24 (8.3%) New Zealand skulls were misclassified as SW African but they were never mistaken for SE Pacific animals. Two skulls out of 22 (9.2%) from SW Africa were erroneously assigned, one each to the New Zealand and Peru stocks. The highest percentages of misclassifications (10.4% and 14.3%) occurred among

Table 5

Geographic variation in cranial characters of mature *Lagenorhynchus obscurus* (N = 298) from Peru, Chile, southwestern Africa and New Zealand. Sexes were pooled after removal of sexually dimorphic variables (see Table 3). NS = not significant, $P>0.05$.

	ANOVA			ANCOVA	
Variable	*F*–ratio	df	*P*	*F*–ratio	*P*
CBL	120.2	3,275	<0.0001	—	—
RL	118.3	3,274	<0.0001	2.48	NS
RWB	10.1	3,287	<0.0001	0.66	NS
RTEN	63.5	3,261	<0.0001	0.83	NS
RTIN	82.4	3,245	<0.0001	1.05	NS
PROW	40.0	3,273	<0.0001	2.46	NS
POOW	44.6	3,264	<0.0001	3.78	<0.02
ZYW	54.5	3,276	<0.0001	4.14	<0.01
PARW	6.88	3,282	<0.0005	0.87	NS
GWPMX	4.39	3,294	<0.005	1.99	NS
ENW	5.35	3,293	<0.0005	1.66	NS
TFW	13.2	3,285	<0.0001	3.65	<0.02
ORL	18.0	3,280	<0.0001	3.31	<0.05
APL	22.9	3,280	<0.0001	3.38	<0.05
INW	34.1	3,282	<0.0001	4.82	<0.005
PTEL	33.5	3,242	<0.0001	2.89	<0.05
UTRL	122.0	3,270	<0.0001	4.33	<0.01
LTRL	109.3	3,242	<0.001	8.92	<0.001
RAL	118.3	3,239	<0.0001	6.18	<0.001
RAH	34.9	3,232	<0.0001	0.14	NS
TCUL	7.4	3,256	<0.0005	6.68	<0.0005
TCUR	9.65	3,256	<0.0001	7.74	<0.0005
TCLL	11.7	3,236	<0.0001	8.85	<0.0001
TCLR	10.1	3,237	<0.0001	8.25	<0.0001
TW	50.3	3,260	<0.0001	25.2	<0.0001
BL	13.9	3,208	<0.0001	0.35	NS
BW	4.1	3,117	<0.02	0.70	NS
HBR	19.5	3,285	<0.0001	4.59	<0.005
LBR	28.4	3,285	<0.0001	1.08	NS
PEL	0.24	3,201	NS	2.31	NS
HCR	6.33	3,235	<0.0005	3.47	NS

Peruvian and Chilean crania, explainable by the relatively greater morphological similarity and geographic proximity. Overall there were successfully identified to geographical population 164 out of 188 (87.2%) of the skulls, increasing to 179 out of 188 (95.2%) when skulls from Chile and Peru were pooled.

Six characters with high discriminatory power were identified from the standardized discriminant function coefficients, *t*-tests and ANOVA's and an additional discriminant analysis was performed using those variables (Table 8). Classification results and the discriminant function plot (Fig. 4) demonstrate that specimen prediction remains fairly effective (143 of 188 or 76.1% and 171 out of 188 or 91.0% when the SE Pacific sample is pooled as one group).

Non-metrical characters

Tooth counts—As expected, tooth counts derived from skulls were consistently greater ($P<0.0001$) than counts made on heads in the flesh because small, apical teeth frequently do not erupt from the gums (see Van Waerebeek, 1992b). Differences of mean tooth counts between skull and fresh specimens varied from 2.29 to 2.67 per jaw arcade. Considering confidence intervals, the best estimate (closest integer) for each of the four arcades was two more teeth visible in skulls than in heads in the flesh.

Tooth counts are bilaterally symmetrical in upper and lower jaws and for all sample pairs (*t*-tests, $P>0.16$). The upper jaw has significantly more teeth than the lower jaw, (one-sided *t*-tests; $P<0.005$ in all cases); confidence intervals included one (tooth) as the largest integer but not zero.

Sexual dimorphism—The 28 non-metrical cranial characters (NMC) tested are, without exception, independent of sex (chi-square contingency tests, $P>0.05$). Sexual dimorphism neither exists in the number of teeth in Peruvian dusky dolphins, both as counted from skulls and from fresh animals (*t*-tests, $P>0.25$). It is considered safe to assume that this is generally true for the other populations of *L. obscurus* and therefore the sexual factor is disregarded in the subsequent analyses.

Developmental variation—Twenty-two of the 28 NMC characters tested (78.6%) in Peruvian dusky dolphins are independent of maturity status (Table 9). Variables which may be correlated with age to some degree (chi-square, $P<0.05$) include position of the left premaxillary foramen at the base of the prenarial triangle (1L), presence of fenestration(s) in occipitals (18L) or basisphenoid (30), visibility of palatine spine (25), and the number of mental foramina (33L). At least one of these is expected to be due to chance fluctuation ($\alpha=0.05$). The more frequent occurrence of a notch in the upper margin of the foramen magnum (17) in immature animals as compared to adults proved highly significant (chi-square=8.83, $P<0.005$).

Geographic variation—The six growth dependent characters were removed from the data set before variation between populations was tested. By doing this, samples available for geographic variation analysis were greatly enhanced as juvenile specimens (but not neonates) could be included. Table 10 lists absolute

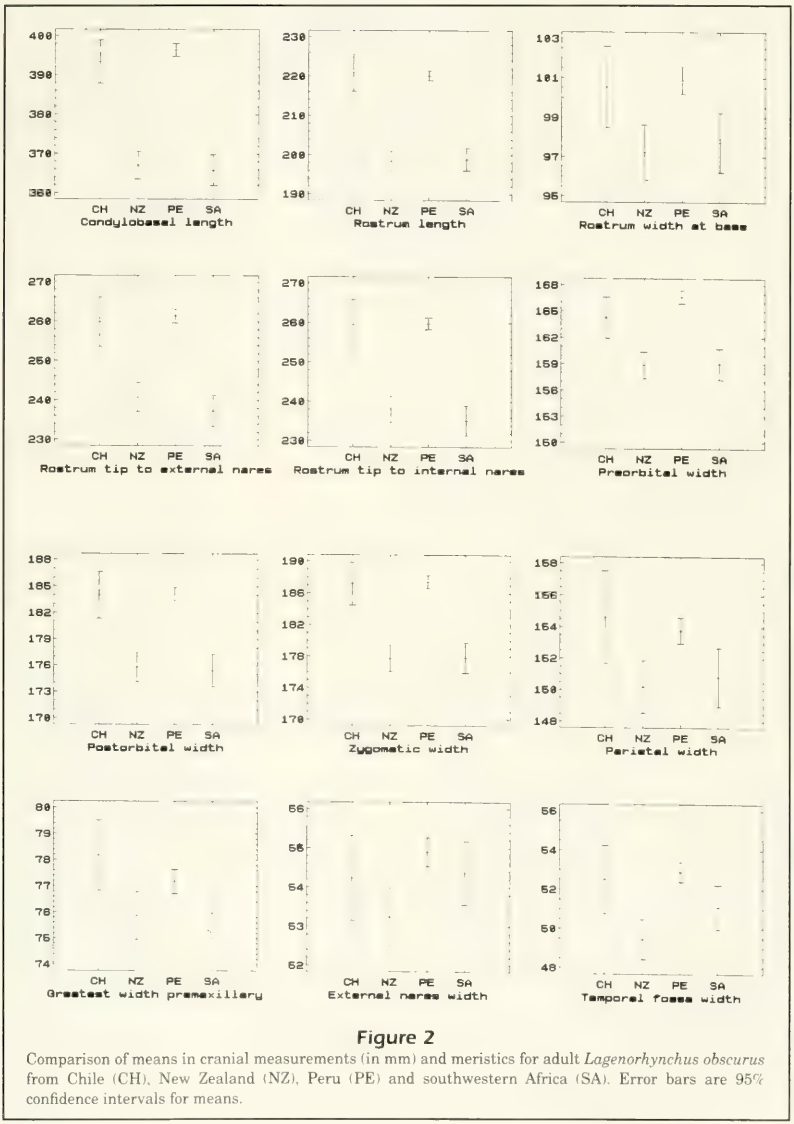

Figure 2

Comparison of means in cranial measurements (in mm) and meristics for adult *Lagenorhynchus obscurus* from Chile (CH), New Zealand (NZ), Peru (PE) and southwestern Africa (SA). Error bars are 95% confidence intervals for means.

frequencies of NMC character states in skulls from Peru (N=221), Chile (N=40), New Zealand (N=69), and southwestern Africa (N=65). Surprisingly, only three characters out of 22 (14%) were found to demonstrate significant differences between geographic groups (chi-square contingency analysis; see Table 10). These are relative position of the foramen in the right premaxillary at the base of the prenarial triangle (variable 1R,

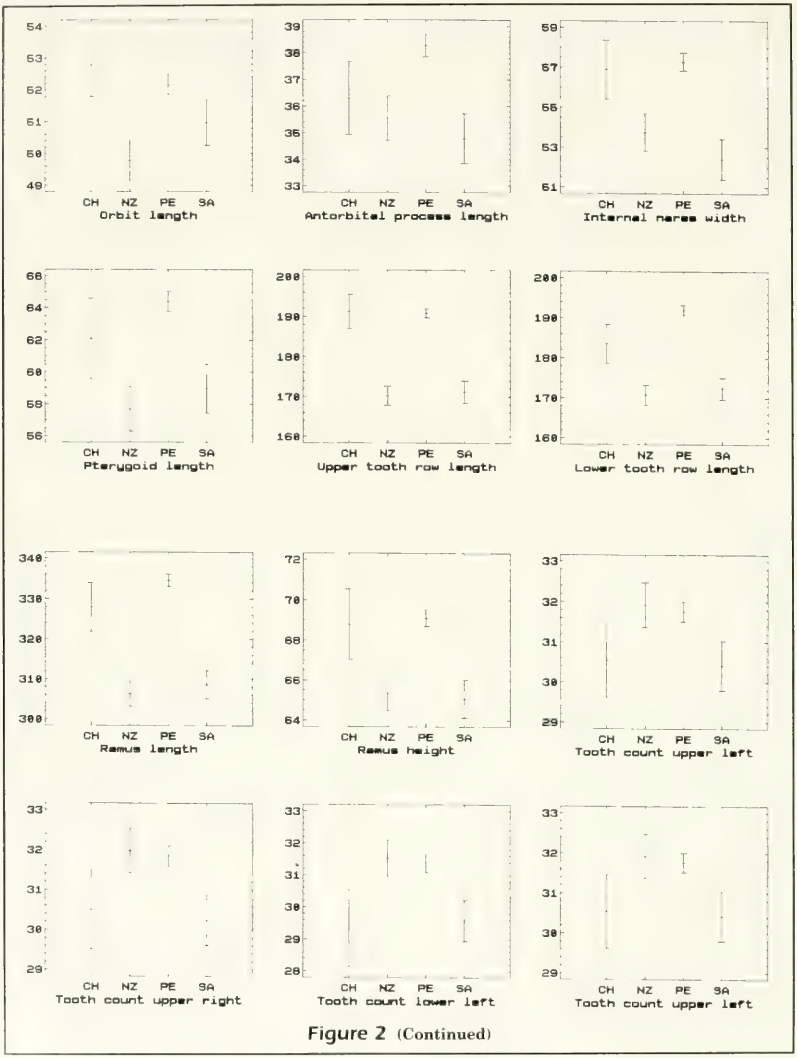

Figure 2 (Continued)

$P<0.0001$), presence of an accessory foramen above the foramen magnum (variable 16, $P=0.02$), and the degree of contact, posteriorly, between pterygoid hamuli (variable 23, $P=0.03$).

Upon comparison of frequencies for variables 16 and 23, two similarity pairs became apparent: New Zealand/southwestern Africa and Peru/Chile. Within each subgroup the monomorphic status for both characters was confirmed (chi-square, df=1, $P>0.41$ in four tests). Southwest African *L. obscurus* differed very significantly in character 1R from all other stocks. By removing the African subsample, frequencies for 1R in the three remaining geographic units became homogeneous (chi-square=0.58; df=4, $P=0.96$).

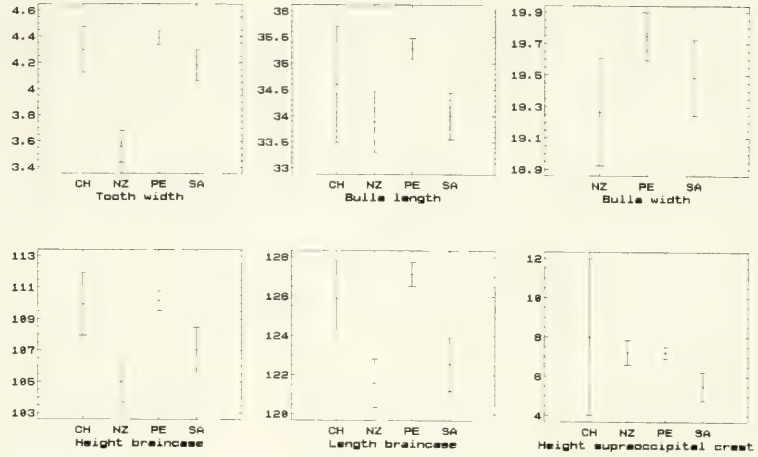

Figure 2 (Continued)

Discussion

Advanced fusion in the frontal-supraoccipital suture (FROC) is the most reliable single cranial criterion of sexual maturity in the dusky dolphin (95% efficiency). In combination with fusion=2 in LAC and ZYG cranial sutures, it can select sexually adult specimens from an undocumented series of *L. obscurus* skulls with even a higher degree of certainty. Distal fusion of premaxillary and maxillary bones has served as the indicator of choice for sexual maturity in *Stenella* spp. (Dailey and Perrin, 1973; Perrin, 1975a; Schnell et al., 1982[8]; Douglas et al., 1984, 1986; Perrin et al., 1981, 1987, 1989), common dolphin (Evans, 1975, 1982), and bottlenose dolphin (Walker, 1981[7]; Mead and Potter, 1990; Van Waerebeek et al., 1990). Its reliability and usefulness however depends on the species and the requirements of selection; Mead and Potter (1990) for instance reported that some immature *Tursiops* skulls were erroneously assigned to the adult group. Almost half of sexually mature dusky dolphins did not show any rostral distal fusion. The character reportedly was of no use in physically mature Pacific white-sided dolphins *Lagenorhynchus obliquidens* (Walker et al., 1986). Classification of specimens with heavily eroded sutures from weathering, boiling or chemical treatment is difficult, and if available sample size permits, these skulls should probably not be used. Moderate heating applied over short periods, to soften tissues for instance, inflicts little damage.

Skulls of *L. obscurus* exhibit little sexual dimorphism, therefore it was not possible to define usable classification functions for sexing specimens. Of 28 non-metrical cranial characters, none exhibited dimorphism. In addition, the number of dimorphic metrical characters (6 of 37, 16.2%) was remarkably low in comparison with that in other small delphinids such as the pantropical spotted dolphin *Stenella attenuata* (23 of 36, 63.9%; Schnell et al., 1985) and the spinner dolphin *Stenella longirostris* (13 of 36, 36.1%; Douglas et al., 1986). *L. obscurus* and the named *Stenella* spp. share the characteristic of males having a broader rostrum and a longer temporal fossa than females, while the overall skull size is not different between sexes (see Schnell et al., 1985; Douglas et al., 1986). Intersexual differences in these species may be governed, at least partly, by similar selection factors. A number of authors have invoked common (genetic) ancestry between *L. obscurus* and the *Stenella* species group to explain certain morphological similarities (True, 1889; Fraser, 1966; Fraser and Purves, 1960; Mitchell, 1970). However, I concur with the opinion of W. F. Perrin[13] that con-

[13]W. F. Perrin, Natl. Mar. Fish. Serv. Pers. commun. March 1992.

Table 6

Geographic variation in skull measurements and meristics of *Lagenorhynchus obscurus* from Peru (PE, N=189), Chile (CH, N=22), New Zealand (NZ, N=47) and southwestern Africa (SA, N=40).

	PE versus CH		NZ versus SA	
Variable	t	P	t	P
CBL	–0.48	0.40	0.48	0.63
RL	0.03	0.98	–0.26	0.80
RWB	–0.67	0.50	–0.45	0.65
RTEN	–1.12	0.27	1.6	0.11
RTIN	–0.34	0.73	1.32	0.19
PROW	2.50	<0.05	–0.094	0.93
POOW	–0.41	0.68	0.29	0.77
ZYW	–0.53	0.60	–0.074	0.94
PARW	0.84	0.40	–0.52	0.60
GWPMX	0.69	0.49	–0.14	0.89
ENW	–1.33	0.19	–2.02	<0.05
TFW	–0.11	0.91	–2.18	<0.05
ORL	1.03	0.30	–2.38	<0.05
APL	–2.89	<0.005	1.11	0.27
INW	–1.07	0.29	2.32	<0.05
PTEL	–2.23	<0.05	–1.28	0.21
UTRL	–0.17	0.87	–0.56	0.58
LTRL	–3.29	<0.005	–0.86	0.39
RAL	–2.10	<0.05	–0.97	0.36
RAH	–0.50	0.62	0.41	0.68
TCUL	–2.71	<0.01	3.45	<0.001
UR	–2.70	<0.01	4.25	<0.0001
TCLL	–3.01	<0.005	4.24	<0.0001
TCLR	–2.76	<0.01	3.95	<0.0002
TW	–1.05	0.30	–7.14	<0.0001
BL	–1.32	0.19	0.33	0.74
BW	—	—	–1.12	0.27
HBR	0.09	0.93	–2.09	<0.05
LBR	–1.37	0.17	–1.02	0.31
PEL	0.52	0.61	1.0	0.33
HCR	—	—	3.43	<0.005

vergence or parallellism is a more likely cause of the cited resemblances. The near absence of sexual dimorphism in the skull and external features of the dusky dolphin, coupled to the exceptionally large relative testis size, led me to suggest that sperm competition should occur in this species (Van Waerebeek, 1992b).

Both bivariate and multivariate analysis provide evidence of extensive geographic variation in skull morphology among the dusky dolphin stocks studied. Most strikingly, adult skulls from the Southeast Pacific stock are considerably larger than either New Zealand or SW African specimens (difference in weighted CBL means is 31 mm or 8.5% of CBL); skulls from New Zealand do not differ significantly in size from those of SW Africa. This is corroborated by the greater mean body length (roughly 10 cm) at sexual maturity and asymptotic length in Peruvian dolphins than in SW African and New Zealand specimens (Van Waerebeek, 1992b). Two non-metrical cranial characters also support the existence of the Peru/Chile and New Zealand/

Table 7

Statistics for discriminant analysis utilizing 21 cranial characters of adult *Lagenorhynchus obscurus* skulls from Chile (CH, N=7), New Zealand (NZ, N=24), southwestern Africa (SA, N=22) and Peru (PE, N=135). Group numbers (under centroids) refer to these used in the discriminant function plot (Fig.3). SEP= Southeast Pacific (Chile and Peru combined).

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation
1	2.202	76.02	0.829
2	0.523	18.06	0.586
3	0.171	5.91	0.382

Unstandardized discriminant function coefficients

	1	2	3
CBL	0.0096	–0.0466	–0.0730
RL	0.0134	0.0025	0.0672
RWB	0.0038	–0.0618	–0.0057
RTEN	–0.0074	–0.0209	0.0268
PROW	–0.0285	–0.0416	–0.0647
POOW	0.0191	0.0528	–0.1291
ZYW	0.0152	–0.0285	0.1545
GWPMX	–0.0204	0.0431	0.0021
ENW	–0.0031	0.1414	–0.0817
TFW	0.0635	0.0256	–0.0028
ORL	–0.0190	0.0361	0.1625
APL	0.0683	–0.0198	–0.0739
INW	0.0481	–0.1066	0.0586
UTRL	0.0209	–0.0352	0.1097
LTRL	0.0664	0.0670	–0.1218
RAL	0.0067	0.0118	0.0047
TCUL	0.0195	–0.0537	–0.0424
TCUR	–0.1049	–0.1707	–0.1628
TW	0.6215	1.7912	0.6270
HBR	–0.0044	0.0669	–0.0467
LBR	0.0276	0.0058	0.0239
CONSTANT	–33.9754	5.8979	15.3204

Classification results

	Predicted group (percentage)				
Actual group	CH	NZ	SA	PE	SEP
CH	85.7	0	0	14.3	100
NZ	0	91.7	8.33	0	0
SA	0	4.6	90.9	4.6	4.6
PE	10.4	1.5	2.2	85.9	96.3

Group centroids

	Discriminant functions		
	1	2	3
CH (=1)	0.398	–0.705	2.040
NZ (=2)	–2.773	–1.254	–0.182
SA (=3)	–2.345	1.582	0.133
PE (=4)	0.855	0.0016	–0.095

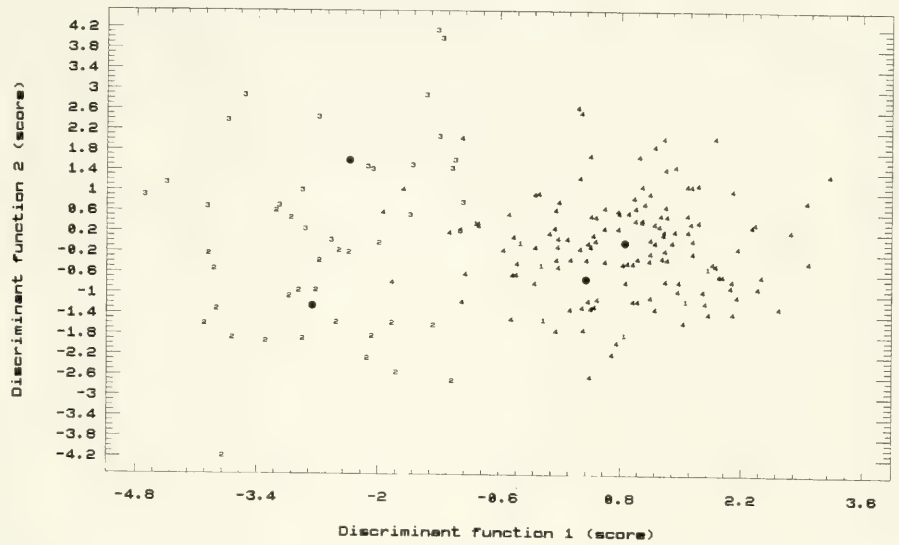

Figure 3

Scores of discriminant functions I and II based on 21 cranial characters for adult skulls of *Lagenorhynchus obscurus* from Chile (1), New Zealand (2), southwestern Africa (3), and Peru (4). Group centroids are indicated by a black dot. Corresponding statistics are presented in Table 7.

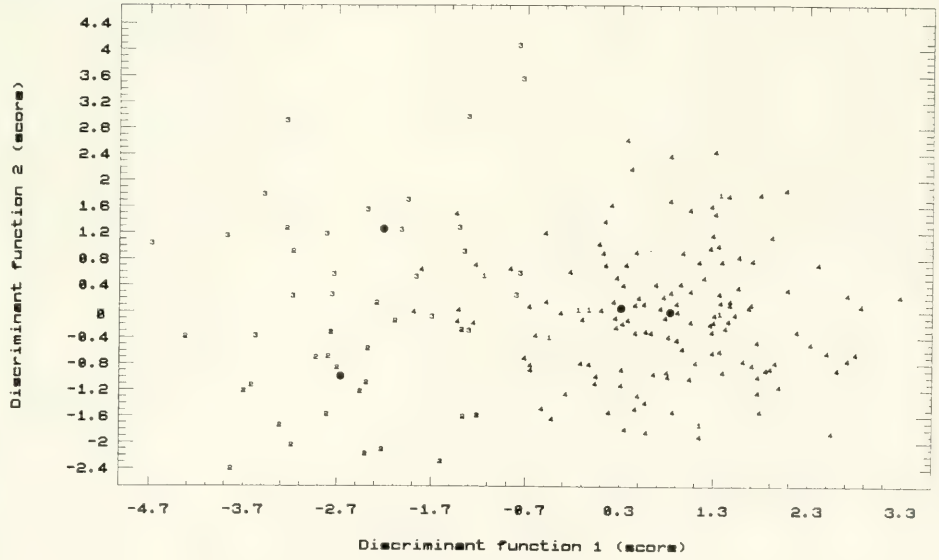

Figure 4

Scores of discriminant functions I and II based on the six most discriminating cranial characters (CBL, PROW, TFW, LTRL, TW, and TCUR) for adult skulls of *Lagenorhynchus obscurus* from Chile (1), New Zealand (2), southwestern Africa (3), Peru (4). Group centroids are indicated by a black dot. Corresponding statistics are presented in Table 8.

Table 8

Statistics of discriminant analysis utilizing a minimum number (6) of sexually monomorphic cranial variables with maximum discriminating power. Samples include adult skulls of *Lagenorhynchus obscurus* from Chile (CH, *N*=7), New Zealand (NZ, *N* =24), southwestern Africa (SA, *N*=22) and Peru (PE, *N*=135).

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation
1	2.0188	84.35	0.818
2	0.3096	12.94	0.486
3	0.0649	2.71	0.247

Unstandardized discriminant function coefficients

	1	2	3
CBL	0.0350	–0.0588	–0.1105
PROW	0.0353	–0.0363	0.1205
TFW	0.0650	0.0484	0.0601
LTRL	0.0663	0.0449	0.1227
TW	0.7749	2.0950	–0.5369
TCUR	–0.0582	–0.3046	0.1422
CONSTANT	–36.6466	18.7270	–5.0552

Classification results

	Predicted group (percentage)				
Actual group	CH	NZ	SA	PE	SEP
CH	71.4	0	0	28.6	100
NZ	0	87.5	12.5	0	0
SA	9.1	18.2	72.7	0	9.1
PE	19.3	2.2	3.7	74.8	94.6

Group centroids

	Discriminant functions		
	1	2	3
CH (1)	0.301	0.0355	–1.281
NZ (2)	–2.674	–0.986	0.0236
SA (3)	–2.218	1.235	0.0400
PE (4)	0.821	–0.0278	0.0557

SW Africa similarity pairs. The New Zealand form is set apart from all others by minimal tooth size and is further distinguished from the SW African form by the significantly higher number of teeth.

A commonly used criterion of subspecific level difference between populations is whether or not 90% of the specimens can be unequivocally assigned to the proper group (Mayr, 1970). Perrin (1975a, 1990), for instance, described three subspecies of spinner dolphin, *Stenella longirostris*, based on this principle. Discriminant analysis allows correct identification of a group (96.5%, 91.7%, and 90.9%) of *L. obscurus* skulls from respectively the Southeast Pacific, New Zealand, and SW Africa, which warrants allocation of subspecific status. It seems premature, however, to formally describe subspecies and assign trinomial names, because no skulls from Argentina have been studied and the Chilean sample was too small to permit definitive conclusions on the degree of heterogeneity in the Southeast Pacific group. In particular, no skulls have been examined from dusky dolphins occurring off southern Chile (south of 46°S), which are thought to belong to the Argentinian stock (Van Waerebeek, 1992a). Considering the persisting mortality levels in gillnet and harpoon fisheries off Peru and northern Chile and in purse-seine operations off Argentina (Van Waerebeek and Guerra, 1986[5]; Guerra et al. 1987; Crespo and Corcuera, 1990[14]; Van Waerebeek and Reyes, 1993; Van Waerebeek, unpubl. data), the question of separate subspecies or population status is of major importance with respect to conservation.

The MANOVA results, suggesting some seasonal morphological variation in *L. obscurus* caught off central Peru, were not confirmed by other tests. However, the picture may be blurred by multi-year pooling or other sampling bias. High-resolution molecular techniques, such as DNA-fingerprinting, should preferably be used to explore this issue.

Although results were complementary, the resolving power of non-metrical cranial characters (not including tooth counts) was inferior to that of measurements (i.e., fewer characters differed); therefore non-metrical characters are not recommended as sole method for subspecific discrimination. Based on studies of the common dolphin, *Delphinus delphis*, Perrin et al. (1989) independently concluded that non-metrical characters be used only in combination with metrical characters and that special attention be paid to controlling conditions to maximize comparability of data sets.

Although little information is available on parasite prevalences in dusky dolphins other than these from Peru, preliminary indications of differential infestations add weight to the morphological findings. Crassicaudid nematodes were practically absent in the cranial sinuses of many hundreds of Peruvian dusky dolphins but were retrieved from the cranial sinuses of one out of two specimens from SW Africa.

[14]Crespo, E. A., and J. F. Corcuera. 1990. Interactions between marine mammals and fisheries in some fishing areas of the coast of Argentina and Uruguay. Doc. SC/090/G2 presented to the IWC, La Jolla, CA, 20–21 October 1990.

Table 9

Frequency distributions for selected non-metrical character states (coded 1–6, see Perrin et al., 1982) in 173 mature (MAT) and 48 immature (IMM) skulls of *L. obscurus* (sexes pooled) from central Peru. Chi-square contingency analyses indicate levels of developmental variation. For df=1, a Yates' corrected chi-square was computed and the higher of the two values (lower *P*) tabulated. Characters are explained in Table 1.

		Non-metrical character states								
		1	2	3	4	5	6	χ^2	*P*	df
1L	MAT	72	61	40				8.5	0.014	2
	IMM	14	28	6						
1R	MAT	56	17	99				4.89	0.09	2
	IMM	22	7	19						
2L	MAT	5	167	1				1.71	0.43	2
	IMM	0	48	0						
2R	MAT	9	162	2				3.21	0.20	2
	IMM	0	48	0						
3	MAT	45	83	45				5.36	0.07	2
	IMM	6	23	19						
5L	MAT	5					166	0.09	0.77	1
	IMM	1					46			
5R	MAT	2	1				168	0.52	0.77	2
	IMM	1	0				46			
6L	MAT	147	22	3			1	1.14	0.77	3
	IMM	42	6	0			0			
6R	MAT	162	10				1	1.38	0.50	2
	IMM	47	1				0			
9L	MAT	2	171					0.56	0.45	1
	IMM	0	48							
9R	MAT	6	166					1.72	0.19	1
	IMM	0	48							
10	MAT		172					—	—	—
	IMM		48							
12L	MAT	173								
12R	MAT	172						—	—	—
	IMM	48								
13	MAT	1		165	1			0.58	0.75	2
	IMM	0		48	0					
16	MAT	3	170				0.84	0.36	1	
17	MAT	77	96					8.83	0.003	1
	IMM	33	15							
18L	MAT	35	2				133	7.3	0.026	2
	IMM	8	4				36			
18R	MAT	41	3				126	0.97	0.61	2
	IMM	11	2				35			
19	MAT		2				169	0.57	0.45	1
	IMM		0				48			
23	MAT	149	5					1.36	0.24	1
	IMM	38	3							
24	MAT	123	34					3.15	0.08	1
	IMM	38	4							
25	MAT	118	38					5.97	0.01	1
	IMM	39	3							
30	MAT	9	158	0				6.20	0.04	2
	IMM	0	43	1						
33L	MAT		7	48	60	22	3	11.2	0.02	4
	IMM		0	24	12	2	1			
33R	MAT	1	12	52	52	18	4	4.57	0.47	5
	IMM	0	1	17	13	8	0			
34L	MAT	115	23	1				1.25	0.53	2
	IMM	35	4	0						
34R	MAT	118	21	0				1.43	0.23	1
	IMM	36	3	0						

Table 10

Geographic variation in non-metrical cranial (NMC) characters for 395 skulls of *Lagenorhynchus obscurus* from Peru (PE, N =221), Chile (CH, N =40), New Zealand (NZ, N =69), and southwestern Africa (SA, N =65). Frequency distributions of NMC states (coded 1–6, see Perrin et al. 1982) for each region and results of chi-square contingency analyses are presented. Samples include all sex/maturity groups except neonates; characters known to be maturity dependent (see Table 9) have been excluded.

NMC	REG	1	2	3	4	5	6	χ^2	P	df
1R	PE	78	24	118				31.8	<0.0001	6
	CH	10	4	16						
	NZ	21	6	37						
	SA	24	22	15						
2L	PE	5	215	1				2.8	0.83	6
	CH	0	30	0						
	NZ	1	62	0						
	SA	0	61	0						
2R	PE	9	210	2				5.9	0.43	6
	CH	0	30	0						
	NZ	1	62	0						
	SA	0	61	0						
3	PE	51	106	64				5.9	0.43	6
	CH	7	17	6						
	NZ	17	33	13						
	SA	11	27	23						
5L	PE	6	0				212	8.33	0.21	6
	CH	1	0				26			
	NZ	0	0				62			
	SA	3	1				55			
5R	PE	3	1				214	10.8	0.10	6
	CH	1	1				25			
	NZ	0	0				62			
	SA	3	0				57			
6L	PE	189	28	3			1	7.9	0.54	9
	CH	23	5	0			1			
	NZ	51	12	0			0			
	SA	49	10	0			1			
6R	PE	209	11				1	0.89	0.99	6
	CH	27	2				0			
	NZ	59	3				0			
	SA	57	3				0			
9L	PE	2	219					3.85	0.28	3
	CH	1	26							
	NZ	0	63							
	SA	0	60							
9R	PE	6	214					4.94	0.18	3
	CH	3	24							
	NZ	2	60							
	SA	3	57							
10	PE		220					–	—	—
	CH		28							
	NZ		64							
	SA		60							
12L	PE	221	0					7.38	0.06	3
	CH	27	0							
	NZ	61	1							
	SA	57	2							
12R	PE	220	0					7.38	0.06	3
	CH	28	0							
	NZ	62	1							
	SA	57	2							

Table 10 (Continued)

NMC	REG	1	2	3	4	5	6	χ^2	*P*	df
13	PE	1		213	1			2.41	0.88	6
	CH	0		25	0					
	NZ	1		62	0					
	SA	0		59	0					
16	PE	3	218					9.59	0.02	3
	CH	0	21							
	NZ	3	59							
	SA	5	53							
18R	PE	52	5	0			161	7.06	0.32	6
	CH	2	1	0			15			
	NZ	12	0	0			47			
	SA	7	0	1			48			
19	PE	0	2				217	6.48	0.37	6
	CH	0	0				16			
	NZ	0	0				60			
	SA	1	0				55			
23	PE	187	8					8.83	0.03	3
	CH	12	1							
	NZ	41	6							
	SA	41	7							
24	PE	161	38					3.8	0.28	3
	CH	12	2							
	NZ	34	13							
	SA	34	14							
33R	PE	1	13	69	65	26	4	7.24	0.95	15
	CH	0	0	7	4	1	0			
	NZ	0	5	16	16	5	1			
	SA	0	5	24	18	3	1			
34L	PE	150	27	1				8.59	0.20	6
	CH	5	5	0						
	NZ	36	8	0						
	SA	41	9	0						
34R	PE	154	24	0				2.41	0.49	3
	CH	10	3	0						
	NZ	36	8	0						
	SA	47	5	0						

Cyamid amphipods have never been found on *L. obscurus* from Peru (Van Waerebeek, 1992b), whereas in New Zealand they seem to be fairly common (Cipriano, 1985).

The actual distribution of *L. obscurus* populations is generally comparable to that of the four species of *Cephalorhynchus*, and the geographical dispersion may have similarly evolved under the influence of the eastflowing Westwind Drift, as proposed for *Cephalorhynchus* spp. by van Bree (1986) and Robineau (1989). The close affinity of the large-bodied Peruvian dusky dolphin with the Pacific white-sided dolphin (Webber, 1987; Van Waerebeek, 1992b) suggests that the former probably represents the most ancestral (plesiomorph) form of dusky dolphin from which the Argentinian, and small-bodied SW African and New Zealand forms were derived.

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Estimation of historical population size of the eastern spinner dolphin *(Stenella longirostris orientalis)*

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Abstract.—An assessment of the population status of the eastern spinner dolphin (*Stenella longirostris orientalis*) in the eastern tropical Pacific is required by the U.S. Marine Mammal Protection Act (MMPA), because dolphin are killed in the tuna purse-seine fishery. A pooled estimate of abundance from recent (1986–90) research vessel surveys, in combination with estimates of fisheries kills from tuna vessel observer data, was used to estimate the historical (pre-exploitation) population size with a population dynamics model. Estimates of relative population size (current population size divided by historical population size) were calculated by using a range of values for the maximum net recruitment rate and the maximum net productivity level (MNPL). The resulting estimates of relative population size ranged from 0.32 to 0.58, with a best estimate of 0.44 based on available life history data. Estimates of relative population size were all below the value of MNPL used to calculate each estimate. Calculation of confidence limits for relative population size by Monte Carlo simulation showed that the precision of the estimates was sufficient to make a status determination. The results indicated that, as of 1988, the stock of eastern spinner dolphin was depleted as defined by the U.S. MMPA.

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The range of the eastern spinner dolphin, *Stenella longirostris orientalis* (Perrin, 1990), is entirely contained within the eastern tropical Pacific (Fig. 1). An assessment of population condition or status of this stock is required under the U.S. Marine Mammal Protection Act (MMPA), because eastern spinner dolphins are killed in the tuna purse-seine fishery, which includes some U.S. vessels, that occurs in this region. The MMPA requires that each marine mammal population be maintained at an "optimum sustainable population" (OSP) level, which has been defined by the U.S. National Marine Fisheries Service as a population size between the maximum net productivity level (MNPL) and carrying capacity (Federal Register, 21 December 1976, 41FR55536). Therefore, assessing the status of a marine mammal stock involves, if possible, determining if it is above its MNPL. Populations shown to be below MNPL are considered depleted under the MMPA.

One method for determining a population's status relative to MNPL is to estimate historical abundance, meaning abundance prior to significant fisheries mortality, which is assumed equivalent to the equilibrium population size (i.e., carrying capacity). The current population size is then compared with what is thought to be the MNPL for the population, given the estimate of equilibrium population size (Gerrodette and DeMaster, 1990). The historical abundance of several cetacean populations has been estimated by back-calculating from a current abundance estimate, with a population model and annual records of the number of animals harvested (Reilly, 1981; Breiwick et al., 1980, 1984; Lankester and Beddington, 1986). Smith (1983) described a method for back-calculating historical population size (N_h) for spinner and spotted dolphins (*Stenella* spp.) from estimates of the current population size (N_c), the historical kill in the tuna fishery, the maximum net recruitment rate (R_m), and the maximum net productivity level. He used this technique to estimate historical abundance for the eastern spinner dolphin, resulting in estimates of relative population size (N_c/N_h) for 1979 ranging from 0.17 to 0.25.

An estimate of N_h for a population of spinner or spotted dolphins, which have a relatively low R_m, can be very sensitive to the estimate of N_c, as long as the time period between N_c and N_h is not too great (Smith and Polacheck, 1979). Over a long time period (138 years), the estimate of N_h has been shown to be insensitive to the estimate of N_c for a baleen whale (*Balaena mysticetus*) population with a similarly low R_m (Breiwick and Braham, 1990). However, for a population that has experienced a relatively recent decline from known losses, the estimate of N_h should still be sensitive to the estimate of N_c (Gerrodette and DeMaster, 1990).

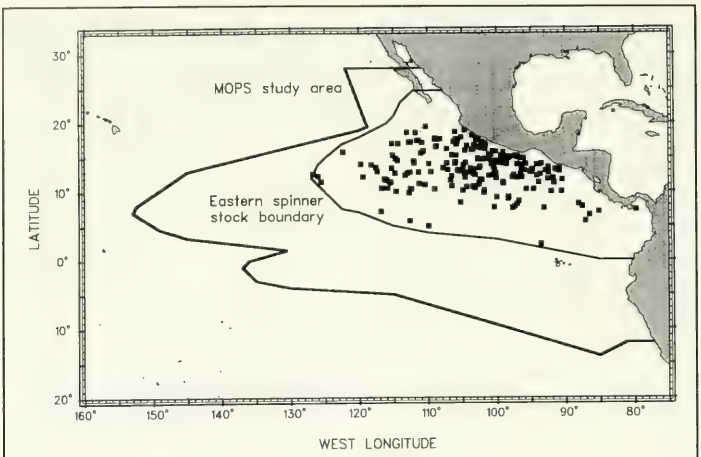

Figure 1

Distribution of the eastern spinner dolphin (*Stenella longirostris orientalis*) in the eastern tropical Pacific. Squares represent positions of all sightings from the 1986–90 Monitoring of Porpoise Stocks (MOPS) surveys used in the abundance estimate (a total of 236 sightings). The outer grey line represents the MOPS study area, and the inner solid line represents the area occupied by the eastern spinner dolphin.

For N_r, Smith (1983) used an estimated abundance of 293,000 animals for the eastern spinner dolphin, which was based on combined data from aerial and research vessel surveys conducted in 1979 (Holt and Powers, 1982). Recently, the U.S. National Marine Fisheries Service conducted large-scale research vessel surveys annually for five years (1986–90) as part of the Monitoring of Porpoise Stocks (MOPS) program, resulting in a revised estimate of abundance of 632,700 (Wade and Gerrodette, 1992b[1]). For a number of reasons, discussed below, this estimate should be more reliable (both more precise and less biased) than the 1979 estimate of abundance used by Smith (1983).

This revised abundance estimate was sufficiently different from the 1979 estimate to justify re-estimation of historical population size for the eastern spinner dolphin. Additionally, estimates of the historical kill have also been revised since Smith (1983), although they did not differ greatly from the previous estimates (Lo and Smith, 1986; Wahlen, 1986). Therefore, I estimated the historical population size for the eastern spinner dolphin using the same methods and the same ranges for the parameters R_m and MNPL as Smith (1983), but with revised abundance and fishery mortality estimates. This resulted in new estimates of relative population size for this stock.

Confidence limits for the estimates of relative population size were calculated by using Monte Carlo simulation methods (Buckland, 1984). These confidence limits only incorporated uncertainty due to sampling error of the current population estimate and the mortality estimates. They did not incorporate uncertainty in the model parameters R_m and MNPL. Therefore, confidence intervals were calculated for all parameter combinations.

Population abundance estimate

The MOPS cruises (1986–90) had approximately five times more kilometers of survey effort in the region occupied by eastern spinner dolphins than the 1979 survey. About 75% of the 1979 survey was concentrated within 1,000 km of the coast, whereas the range of the eastern spinner dolphin is up to 2,000 km from the coast (Fig. 1, Perrin et al., 1985). Therefore, the 1979 survey provided little coverage of the western half of the area occupied by eastern spinner dolphin (Holt and Powers, 1982, fig. 1). Raw sample sizes show the large difference in the quantity of data: a total of 285 schools containing eastern spinner dolphins were recorded during the MOPS surveys; a total of only 41 schools, during the 1979 survey. The large increase in

[1]Wade, P. R., and Gerrodette, T. 1992b. Estimates of cetacean abundance in the eastern tropical Pacific. Paper SC/44/018 presented at the annual meeting of the Int. Whal. Comm., June 1992.

the quantity of data made the MOPS estimates of abundance more precise for this stock, whereas the increased coverage of the stock range reduced the potential bias of geographical variation in abundance.

Both Holt and Powers (1982) and Wade and Gerrodette (1992b[1]) used line-transect analysis methods (Burnham et al., 1980) to estimate abundance. However, the relatively low number of sightings that resulted from the 1979 survey required an analysis technique that pooled sightings of different stocks and species of dolphin to estimate the abundance of each stock (Holt and Powers, 1982). Although the same technique was used initially to estimate annual abundance for the first four years of the MOPS data (Holt and Sexton, 1989, 1990, a and b; Gerrodette and Wade, 1991), the greater number of sightings in each year made this unnecessary. Therefore, to examine trends in abundance, a revised analysis of all five years of MOPS data was undertaken in which annual estimates of abundance for each stock were made only from sightings of that stock (Wade and Gerrodette, 1992a). These estimates were considered to be less biased estimates of abundance than earlier estimates available for eastern tropical Pacific dolphins (IWC, 1992). No significant trend in abundance for eastern spinner dolphins was observed over this short period, but the power of detecting a trend was low (Gerrodette, 1987; Wade and Gerrodette, 1992a). The five annual estimates of abundance for the eastern spinner dolphin ranged from 391,200 to 754,200, with a mean of 588,500.

Wade and Gerrodette (1992a) discussed in detail the differences between their analysis technique and the Holt and Powers (1982) technique, but I will briefly summarize the two major differences here. First, Holt and Powers (1982) calculated a single effective strip width (i.e., 2.0/f(0), Burnham et al., 1980) for all dolphin species, whereas Wade and Gerrodette (1992a) estimated a separate value for each stock. These effective strip widths varied substantially between the different dolphin stocks, ranging from a low of 2.5 km to a high of 11.9 km (Wade and Gerrodette, 1992a), indicating that the Holt and Powers (1982) technique may have introduced considerable bias by pooling across different stocks and species.

Second, Holt and Powers (1982) estimated the abundance of each stock by making a pooled estimate for each species, and then divided the species estimate between the stocks of that species according to the relative size of the area occupied by each stock. For example, an estimate of spinner dolphin abundance was made by pooling sightings of eastern spinner dolphins with sightings of whitebelly spinner dolphins, a different morphological form that is distributed farther offshore and partially overlaps the area occupied by the eastern spinner dolphin (Perrin et al., 1985, 1991). The abundance estimate for the eastern spinner dolphin was then made by multiplying this pooled estimate by the ratio of the area occupied by the eastern spinner dolphin to the sum of that area plus the area also occupied by the whitebelly spinner dolphin. This approach would only be un-biased if the two stocks had exactly the same density (number of animals per unit area) within their respective stock areas. There is no reason to assume this is true; therefore, an analysis based solely on sightings of eastern spinner dolphin, as in Wade and Gerrodette (1992a), is likely to be less biased.

To obtain a best estimate of absolute abundance, the five years of MOPS data were pooled across years for a second analysis to estimate average abundance for the period for 25 stocks of cetaceans in the ETP, including the eastern spinner dolphin (Wade and Gerrodette, 1992b[1]). The analysis technique of Wade and Gerrodette (1992a) was used, supplemented by a technique for prorating sightings from unidentified categories. Abundance estimate from this analysis should represent the (least biased and most precise) abundance estimate currently available for eastern spinner dolphin, and was therefore used as the starting point for the back-calculations. A summary of the methods and results from that paper for the eastern spinner dolphin has been presented here.

Methods

Pooled (1986–90) abundance estimate

The methods of Wade and Gerrodette (1992a) were mostly repeated but were applied to all five years of data together rather than separately to each year by itself. Population abundance (N) of eastern spinner dolphins was computed by line-transect methods (Burnham et al., 1980) as:

$$N = \sum_{k=1}^{i} N_k, \tag{1}$$

where

$$N_k = \frac{n_k f_k(0)}{2 L_k} S_k A_k \tag{2}$$

and

N_k = abundance estimate for eastern spinner dolphins in stratum k,

n_k = number of eastern spinner dolphin schools in stratum k,

$f_k(0)$ = detection function in stratum k, evaluated at zero distance,

S_k = mean school size for eastern spinner dolphin schools in stratum k,

L_k = total effort in stratum k in kilometers,
A_k = total area in stratum k in square kilometers.

This represents a stratified analysis, where only sightings from a stratum were used to calculate the density and, therefore, abundance within the stratum. Abundance estimates for each stratum were summed across the four strata to get a total estimate for the stock. The only change in methodology from Wade and Gerrodette (1992a) involved the calculation of f(0). In that analysis, f(0) was estimated by pooling across strata because of inadequate sample sizes in each stratum in each year. With the larger sample sizes available from pooling the five years of data, there were enough sightings in the inshore and middle strata (Wade and Gerrodette, 1992a; fig. 1) to estimate f(0) independently in each stratum. A third stratum (west) on the edge of the stock area had only four sightings, so a single pooled estimate of f(0) was estimated for the middle and west strata. As expected, because it was outside of the range of eastern spinner dolphin (Perrin et al., 1985), there were no sightings in the fourth stratum (south). A hazard rate model (Buckland, 1985) was fit to the data to estimate f(0). The perpendicular distances were truncated at 5.5 km, because not all dolphin schools further than 5.5 km perpendicular distance were pursued for species identification and school size estimation.

Eastern and whitebelly spinner dolphins partially overlap in range, but can be distinguished from each other by their color pattern and morphology (Perrin, 1990; Perrin et al., 1991). Out of 134 sightings of spinner dolphins in the area of overlap between the two stocks, 16 were, for various reasons, unidentified to stock. Those sightings were prorated to the eastern stock of spinner dolphin by using the estimated proportion of spinner dolphin in the overlap area from the eastern stock (Wade and Gerrodette, 1992b[1]). Similarly, sightings of unidentified dolphins were prorated to the eastern stock, based on the estimated proportion of dolphins from the eastern stock in each stratum (Wade and Gerrodette, 1992b[1]). The prorated portions of unidentified spinner dolphin and unidentified dolphin were added to the original estimate to give a final estimate of abundance. The standard error of the abundance estimate was calculated by bootstrap methods (Efron, 1982), by using legs of effort as the resampling unit, with 1,000 iterations.

Fisheries kill estimates

Estimates of dolphin kill from the tuna fishery in the ETP have been revised since Smith (1983). Lo and Smith (1986) presented revised kill estimates for 1959–1972, and Wahlen (1986) presented revised kill estimates for 1973–1978, in each case with associated standard errors. Additionally, kill estimates for 1979–87, with associated standard errors, have been published (IATTC, 1989). However, Lo and Smith (1986) reported total dolphin kill and did not divide it into stock categories, while Wahlen (1986) reported kill estimates by stock, but only for the U. S. tuna vessel fleet. Therefore, I divided the estimates of Lo and Smith (1986) to stock by the same stock proportions used in Smith (1983). I adjusted the estimates of Wahlen (1986) using the estimated total number of sets, as reported in Punsly (1983). Wahlen (1986) reported the estimated number of sets by the U.S. fleet. I multiplied the kill estimate in each year from Wahlen (1986) by the ratio of the sets made by the entire fleet to the sets made by the U.S. fleet to produce an estimate of the total number of eastern spinner dolphins killed in each year. This assumes that the kill rates of the unobserved international fleet were the same as the U.S. fleet.

Population model

The methods of Smith (1983) were duplicated, by using the simple recursive relationship

$$N_{t+1} = N_t - K_t + R_t\,(N_t - \tfrac{1}{2}K_t), \tag{3}$$

where
N_t = population abundance in year t
K_t = fisheries kill in year t
R_t = net recruitment rate in year t.

Density-dependence is incorporated into the equation through the net recruitment rate, which is defined as

$$R_t = R_m \left[1 - \left(\frac{N_t}{N_h} \right)^z \right], \tag{4}$$

where
R_m = maximum net recruitment rate
z = shape parameter that sets the maximum net productivity level (MNPL)
N_h = historical population size (assumed to be the equilibrium population size).

For any value of R_m and MNPL, z can be calculated as in Polachek (1982). Equation 1 can be solved for N_t as a function of N_{t+1}, R_t, and K_t. Therefore, by specifying an initial population size, the number of animals killed in each year, the maximum net recruitment rate, and the maximum net productivity level, these two equations can be iteratively solved for N_h.

Estimates of R_m and MNPL

Values used by Smith (1983) for R_m were 0.0, 0.03, and 0.06, which he thought to encompass the range of possible values of R_m for spinner dolphins. No direct estimate of net reproductive rate (R) exists for eastern spinner dolphins because of the difficulty in estimating survival rates. The calving interval is approximately three years (Perrin and Reilly, 1984). The age of sexual maturity (ASM) has been reported as five years (Perrin and Henderson, 1984). However, a new study using a much larger data set estimated ASM for the eastern spinner dolphin to be approximately 10 years, by using data collected from 1974 to 1990[2]. This is similar to the estimate of approximately 11 years for the congener northern spotted dolphin, *Stenella attenuata* (Chivers and Myrick, 1991[3]; Myrick et al., 1986), which is found in the same region of the eastern tropical Pacific.

There are no estimates of survival rates for eastern spinner dolphin. Therefore, estimating the net reproductive rate for eastern spinner dolphin required using estimates of survival rates from another species. Among the best estimates of survival rates for a delphinid come from a long-term study of known individuals of a coastal population of *Tursiops truncatus*, with estimates of adult and calf survival of 0.96 and 0.80, respectively (Wells and Scott, 1992). From Reilly and Barlow (1986), those survival rates in combination with a calving interval of three years and an ASM of nine years resulted in an R of 0.03, which could be considered the best estimate of R for the eastern spinner dolphin. Those survival rates may be low, however, because the Wells and Scott (1992) study was of a population that was thought to be at equilibrium, as it had been relatively constant in abundance for many years. Using the maximum survival rates considered by Reilly and Barlow (1986) with the same calving interval (3 yr) and ASM (9 yr) results in an R of 0.05. If the eastern spinner dolphin was well below half its equilibrium population size in 1979 (Smith, 1983), then its net reproductive rate should have been very close to its maximum, R_m. For this paper I therefore considered 0.04 as the best estimate of R_m currently available for the eastern spinner dolphin, with 0.06 the greatest value of R_m possible. Therefore, the same range of values as in Smith (1983) was used for R_m, ranging from 0.00 to 0.06 by increments of 0.002, for a total of 31 values.

Values used by Smith (1983) for MNPL were 0.50, 0.65, and 0.80 (MNPL is expressed as a fraction of equilibrium population size in this paper), corresponding to z values (see Eq. 4) of 1.0, 3.482, and 11.216, respectively. These encompassed the range of actual values of MNPL for long-lived marine mammals, such as dolphins, based on work by Fowler (1981). No direct estimate of MNPL exists for the eastern spinner dolphin. Fowler (1984) gave evidence that MNPL was greater than 0.50 for cetaceans. A value of 0.60 is currently being used for management of cetaceans under the U.S. MMPA (Federal Register, 31 October, 1980, 45FR64548), and for this paper, will be considered the best working value of MNPL currently available for the eastern spinner dolphin. Values of z were used so that MNPL ranged from 0.50 to 0.80 (the same range as in Smith, 1983), by using increments of 0.01, for a total of 31 values. The exact value of z necessary to give the specified MNPL for any value of R_m was calculated as in Polachek (1982).

The 31 values used for both R_m and MNPL produced a total of 961 parameter combinations for which relative population size was estimated. This large number of parameter combinations allowed the calculation of contours for the estimate of relative population size as a function of the 2 parameters of the model.

Confidence limits for N_h

For every combination of the parameters R_m and MNPL, confidence limits for relative population size were calculated by a Monte Carlo simulation (Buckland, 1984) which incorporated the sampling error of the current abundance and kill estimates. On each of 1,000 iterations, an artificial data set was randomly generated by sampling values for the current abundance and for the fisheries kill in each year. These values were each drawn from Gaussian distributions with means and variances equal to the appropriate point estimates. Relative population size was then estimated for each of these artificial data sets, and 95% confidence limits for relative population size were calculated using the percentile method (Efron, 1982).

The kill estimates for 1959–1972 were not independent from each other, as Lo and Smith (1986) estimated the kill in each year by multiplying an average mortality-per-set for 1959–1972 by the number of fishing sets in each year. Therefore, on each simulation iteration the kill values for 1959–1972 were randomly generated with the same random deviate. This resulted in the kill values for those years being perfectly correlated amongst themselves from simulation

[2]Susan Chivers, Southwest Fish. Sci. Cent., La Jolla, CA. Pers. commun.

[3]Chivers, S. J., and A. C. Jr. Myrick. 1991. Comparison of age at sexual maturity for two stocks of offshore spotted dolphins subjected to different rates of exploitation. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-31, 19 p.

trial to trial, which correctly reflected the lack of independence in the actual estimates. The kill values for all other years were sampled independently.

Results

Estimates of abundance and kill

The five years of the MOPS surveys resulted in 236 sightings of eastern spinner dolphins used in the abundance estimate. The abundance estimate based solely on these sightings was 568,100. Adding prorated numbers of unidentified spinner and unidentified dolphin sightings resulted in a final estimate of 632,700, with a CV of 0.167 (Table 1). The fisheries kill estimates ranged from a high in 1961 of 138,000 to a low in 1983 of 700 (Table 2).

Contours of relative population size (N_t/N_h) as a function of R_m and MNPL ranged from 0.35 to 0.55 (Fig. 2). Relative population size increased with both R_m (growth rate) and MNPL (the amount of non-linearity in the density-dependence response). The lowest relative population size was 0.32, for the case of R_m=0.00, (i.e., no net growth in the population before fisheries kill was included). The highest relative population size was 0.58 for the case of the highest growth rate and MNPL (0.06 and 0.80, respectively). These low and high estimates of relative population size correspond to estimates of pre-exploitation abundance of 1,956,000 and 1,100,000, respectively. Relative population size increased by approximately 0.03 for every increase of 0.01 in R_m. The influence of MNPL was greater at higher growth rates, as relative population size increased by approximately 0.02 for every increase of 0.10 in MNPL at R_m=0.02, but increased by approximately 0.05 for every increase of 0.10 in MNPL at R_m=0.06. There were no combinations of parameter values such that relative population size was estimated to be above MNPL.

The upper 95% confidence limit for relative population size as a function of R_m and MNPL, based on the sampling error of the abundance and kill estimates, ranged from 0.45 to 0.91 (Fig. 3). The upper confidence limit was always above MNPL when R_m was greater than 0.046 (Fig. 3, shaded region). The lower 95% confidence limit for relative population size as a function of R_m and MNPL, ranged from 0.22 to 0.36 (Fig. 4).

All population trajectories declined until 1973 (Fig. 5), after which the estimated fisheries kill declined substantially (Table 2). For the highest growth rate, the population trajectory showed an increasing trend from 1976 to 1988 (Fig. 5, line C), whereas for the lowest growth rate the model resulted in a relatively stable population level between 1976 and 1988 (Fig. 5, line A).

The confidence limits around relative population size broadened with increasing R_m. For example, for a MNPL of 0.60, the confidence limits ranged from 0.23 to 0.44 for R_m=0.00, whereas they ranged from 0.33 to 0.72 for R_m=0.06 (Fig. 6). As in Smith (1983), relative population size was a linear function of R_m.

Discussion

For all parameter values of R_m and MNPL equal to those in Smith (1983), estimates of relative population size were higher in this analysis. For example, for R_m=0.03 and MNPL=0.65, Smith (1983) reported a relative population size of 0.20 versus a result of 0.42

Table 1

Estimate of abundance (in thousands of animals) of the eastern spinner dolphin (*Stenella longirostris orientalis*) from the Monitoring of Porpoise Stocks surveys (1986–90). Strata are identified in Figure 1.

	Abundance estimates			
	Total	Inshore	Middle	West
From eastern spinner dolphin schools	568.0	364.8	160.2	43.1
Prorated from unidentified spinner dolphins	15.4	9.0	6.0	0.4
Prorated from unidentified dolphins	49.2	37.5	10.9	0.8
Final estimate	632.7			
Standard error	105.7			
Coefficient of variation	0.167			
Upper 95% confidence limit	778.9			
Lower 95% confidence limit	403.2			

Table 2

Estimates of fisheries kill in thousands by year for the eastern spinner dolphin (*Stenella longirostris orientalis*). CV is the coefficient of variation of the kill estimate. Sources for the estimates are 1) 1959–72 from Lo and Smith (1986), using the stock proportions of Smith (1983); 2) 1973–78 from Wahlen (1986), adjusted for number of sets of total fleet in Punsly (1983); 3) 1979–87 from IATTC (1989). See text for explanation.

Year	Mortality	CV
1959	14.3	0.32
1960	124.3	0.31
1961	138.8	0.28
1962	56.2	0.25
1963	62.4	0.22
1964	101.4	0.20
1965	119.6	0.20
1966	97.2	0.15
1967	66.8	0.16
1968	59.5	0.15
1969	106.0	0.15
1970	107.4	0.15
1971	58.4	0.17
1972	87.4	0.16
1973	18.4	0.16
1974	17.8	0.11
1975	17.1	0.11
1976	14.7	0.12
1977	1.8	0.12
1978	1.1	0.11
1979	1.5	0.24
1980	1.1	0.20
1981	2.3	0.28
1982	2.6	0.33
1983	0.7	0.38
1984	6.0	0.52
1985	8.9	0.16

here. The different results must be due to either the use of revised estimates of abundance and kill or the use of 1988 as a starting point rather than 1979; these were the only differences between the analyses. As will be shown, most of the difference resulted from the higher estimate of current population size, although the lower revised kill estimates also contributed to a higher estimate of relative population size. Repeating the back-calculation of Smith (1983) from 1979, but using revised population and kill estimates, resulted in nearly the same estimate of relative population size as reported here. For example, for R_m=0.03 and MNPL=0.65, back-calculating from 1979 as opposed to 1988 resulted in an estimate of relative population size of 0.41 versus 0.42, whereas Smith (1983) reported a value of 0.20. An inspection of the population trajectories (Fig. 5) confirms that the difference was not due to the different starting year, as the model trajectories, except at the highest growth rates, indicated little change in the population size between 1979 and 1988. This also agrees with the independent results of Buckland et al. (1992), which indicated little difference in relative population size between those two years. Therefore, the difference in the results reported here and those of Smith (1983) should not be interpreted as a recovery in the population between 1979 and 1988. These new, higher estimates of status should instead be interpreted as a revision of the estimate of relative population size, due mostly to the improved abundance estimate available from the MOPS surveys.

The new estimates of relative population size, although higher than Smith (1983), are still below MNPL for all parameter combinations. Because the parameter values used encompassed those values possible for a spinner dolphin (Reilly and Barlow, 1986), this result indicated that, as of 1988, the eastern spinner dolphin was still well below its 1959 population size. With R_m=0.04 and MNPL=0.60, the population was estimated to be at 44% of its historical size. Even with the maximum value of R_m of 0.06, the population in 1988 was estimated to be 43% (MNPL=0.50) to 58% (MNPL=0.80) of its size in 1959. However, careful consideration must be given to several issues before accepting these results as valid. These issues include the precision (reflecting the precision of the abundance and kill estimates) and potential biases (reflecting either biased abundance and kill estimates or mis-specification of the model) of the result, and the quality of pre-1972 fisheries kill data.

Precision

The precision of the estimates of relative population size was investigated by simulation to explore the uncertainty of the results due to sampling error, under the assumptions that the population model and parameter values were true. This addresses the question of how likely the estimates of relative population size were below MNPL if the true relative population size was above MNPL, solely because of variability associated with sampling the current abundance and fisheries kill estimates. The upper 95% confidence limit of relative population size was below MNPL for the majority of the parameter combinations, moving above MNPL only for values of R_m greater than 0.018 (Fig. 3). If MNPL was assumed to be 0.60, then the upper 95% confidence limit of relative population size was only above MNPL for values of R_m greater than 0.034 (Fig. 3). The upper confidence limit was always above MNPL if R_m was at least 0.046. Viewed in a hypothesis testing context, this result indicated that the null hypothesis that relative population size was greater than MNPL in 1988 could be rejected for most of the parameter combinations. Only at higher growth rates could this hypothesis not be rejected. From sampling error alone, it was equally possible that the population was actually worse off than estimated, as the lower 95% confidence limits go as low as 0.22, and were as low as 0.28 even at the highest growth rate of R_m=0.06.

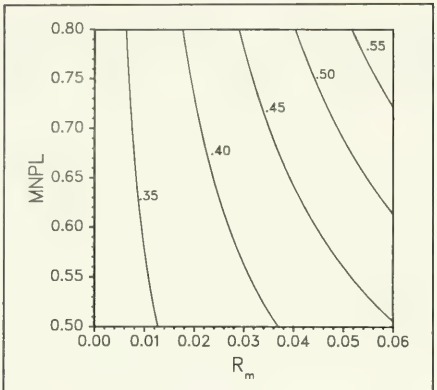

Figure 2

Contours of relative population size (current abundance divided by historical abundance) for the eastern spinner dolphin (*Stenella longirostris orientalis*), as a function of maximum net recruitment rate (R_m) and maximum net productivity level (MNPL).

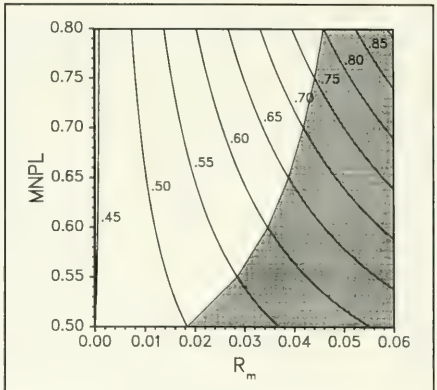

Figure 3

Contours of the upper 95% confidence limit for relative population size for the eastern spinner dolphin (*Stenella longirostris orientalis*), as a function of maximum net recruitment rate (R_m) and maximum net productivity level (MNPL). The shaded region represents the area where the confidence limit was above MNPL.

The confidence limits around relative population size were not much greater proportionally than the confidence limits around N_e (Fig. 6). For example, from the simulation the confidence limits for relative population size with values of 0.04 for R_m and 0.60 for MNPL were 0.29–0.62, representing a coefficient of variation (CV) of 19%, whereas the CV of N_e was 17% (Table 1). Although one might have expected the precision of the estimate of relative population size to be much less than the precision of N_e, this was not the case because of the independence of most of the kill estimates. Sampling variance in the kill estimates would therefore

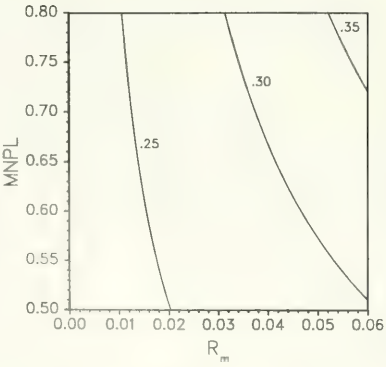

Figure 4

Contours of the lower 95% confidence limit for relative population size for the eastern spinner dolphin (*Stenella longirostris orientalis*), as a function of maximum net recruitment rate (R_m) and maximum net productivity level (MNPL).

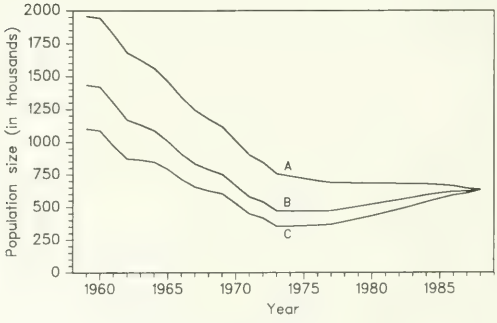

Figure 5

Population model trajectories for the eastern spinner dolphin (*Stenella longirostris orientalis*) for three different parameter combinations of maximum net recruitment rate (R_m) and maximum net productivity level (MNPL): (A) R_m=0.00 and MNPL=0.50, (B) R_m=0.04 and MNPL=0.60, and (C) R_m=0.06 and MNPL=0.80. A and C represent the lowest and highest estimates of relative population size, respectively. B represents the combination of the best estimates for the parameters based on available life history data.

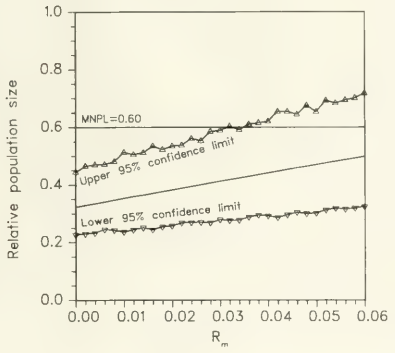

Figure 6

Point estimates and 95% confidence limits for relative population size for the eastern spinner dolphin (*Stenella longirostris orientalis*), as a function of the maximum net recruitment rate (R_m), for the estimate of the maximum net productivity level (MNPL=0.60) currently used for management under the U.S. Marine Mammal Protection Act.

tend to cancel itself, as over-estimates of kill in some years would be balanced by under-estimates in other years. However, systematic bias in the kill estimates would lead to a poor estimate of relative population size, creating a relatively precise yet inaccurate estimate. The same would be true for bias due to the use of an inappropriate model, or in the estimate of N_c. Potential biases in these three areas must therefore be considered.

Bias

Two major sources of bias may have existed in the fisheries kill estimates from 1972 to the present. One source of bias, that of observer effects, has been demonstrated and implies that less dolphin kill occurred on observed trips due to modifications in fishing behavior in response to the observer's presence (Wahlen and Smith, 1985). Unfortunately, there is no way to estimate the magnitude of the effect. The second potential source of bias was the lack of participation in data collection by some countries during some years, especially if significant differences in kill rates existed between countries. Most important may have been the lack of 1979–1986 data from Mexico (Edwards, 1989), a major component of the fishery whose kill rates may have been higher than average during that time period. These biases would lead to under-estimates of kill and thus over-estimates of relative population size.

Additional sources of bias existed in the pre-1972 kill estimates, because of both a lack of observations of mortality-per-set (MPS) in many years and because the MPS data prior to 1971 were not collected as part of a systematic observer program. Data on the number and types of sets were collected in every year, starting in 1959 (Punsly, 1983), but an observer program for collecting MPS data was not started until 1971 and random placement of observers until 1972 (Edwards, 1989). The moderate amount of MPS data collected in 1971 was potentially biased because most of the boats with observers were smaller and older, and may have had a higher MPS (Edwards, 1989; Lo and Smith, 1986, table 1). Most of the pre-1971 data were from scientists who were on the tuna boats for the purpose of collecting dolphin specimens, but who also recorded MPS data on their own initiative (Smith and Lo, 1983). There is no obvious reason why tuna vessels that agreed to allow scientists to collect specimens during their fishing operations would tend to have different mortality rates, but in a strict sense these were not random samples of fishing trips. Data from one fishing trip in 1964 were recorded and reported by a fisherman, who may have done so because of the magnitude of the kill, making those data potentially biased (Smith and Lo, 1983). However, the MPS data did not differ greatly in those years from the data collected in 1972 (Lo and Smith, 1986, table 1). Because of this and the greater quantity of MPS data available from 1972, estimates of 1959–1972 fisheries kill made by multiplying the average 1972 MPS rate by the number of sets in each year would not differ greatly from the estimates used here from Lo and Smith (1986), which were made by using the pooled 1964–1972 MPS rate.

Therefore, the fisheries kill would only have been over-estimated if the MPS in the pre-1971 unobserved years was lower than in 1972. However, MPS has consistently declined over time, declining most rapidly following the passage of the Marine Mammal Protection Act in 1972 (Smith 1983). No evidence exists that MPS could have been lower from 1959 to 1970 than it was in 1971–72. MPS may have been higher, especially before use of the back-down procedure had become widespread and well practiced (Perrin, 1969; Edwards, 1989). If it is assumed that MPS has only declined since the beginning of the fishery, the 1959–1970 kill estimates of Lo and Smith (1986) were likely under-estimates of the true kill. Thus, the major sources of bias in fisheries kill estimates all suggest that kill estimates were negatively biased.

Bias in the estimate of abundance could also bias the estimate of relative population size. Wade and Gerrodette

(1992a) discuss a number of sources of potential bias when applying line-transect theory to the MOPS survey data. Several potential sources of bias do not appear to have a major effect. Independent observer experiments indicate that few schools (and no large schools) were missed on the trackline (Wade and Gerrodette, 1992a). Aerial photographs have confirmed that little bias has been introduced by the observer's estimate of school size (Gerrodette and Perrin, 1991[4]). One partially unresolved issue is that of vessel avoidance by dolphin schools, which would bias the estimate downwards, although this may not have been a major problem (Au and Perryman, 1982; Hewitt, 1985). Additionally, mean school size is likely over-estimated owing to the decreased probability of detection of small schools at larger perpendicular distances (Drummer and McDonald, 1987). Although some stocks in the MOPS surveys appeared to be biased by as much as 20% by this problem, the eastern spinner and other stocks were not (Wade and Gerrodette, 1992a). Finally, the distribution of the eastern spinner dolphin is well known (Perrin et al., 1985) and is well within the MOPS study area (Fig. 1), so it can be concluded that the abundance estimate applies to the entire population. Therefore, the estimate of abundance did not contribute any major bias to the estimate of relative population size.

Bias may also have been introduced by assuming that the simple model specified in Equation 3 correctly models eastern spinner population dynamics, although a simulation study has shown that a simple model can perform as well as a more complex model for this type of analysis (Lankester and Cooke, 1987). The most important feature of eastern spinner population dynamics for this analysis is their inability to undergo large increases in population size from one year to the next. Their relatively low maximum population growth rate, which is due to the biological constraints of their life history discussed above, was incorporated into Equation 3 by using only biologically plausible values of R_m. The only way in which the actual population could have substantially differed from the model would be if the population had a much lower growth rate than expected in some years. For example, large interannual variations in oceanographic conditions related to El Niño events in the eastern tropical Pacific (Fiedler et al., 1992) may lead to large changes in the quantity of prey available for the dolphins. This could lead to lower growth rates in some years, which would cause the specified model to over-estimate relative population size.

Of more concern is the lack of age-structure in the model (Goodman, 1984[5]). The age-distribution of the northern spotted dolphin (*S. attenuata*) kill of 1974 to 1983 was heavily biased towards mature animals (Barlow and Hohn, 1984). If the kill of eastern spinner dolphin was similar for all years, then the simple model used would have over-estimated relative population size. Removing proportionally more mature animals, whose reproductive value was highest, would have temporarily reduced the growth rate of the population and caused the population to decline for a longer period than predicted by the simple model.

In fact, an independent abundance index derived from data on sightings of dolphin schools from tuna vessels estimated that the population experienced a statistically significant decline from 1975, the first year the index was available, until 1982 (Buckland et al., 1992). This is different from the population trajectory I estimated here, which declined only until about 1977 (Fig. 5). Additionally, Buckland et al.'s (1992) trajectory indicated that the population level in 1988 was not substantially different from that of 1979, which conflicts with the model trajectories presented here with higher growth rates (Fig. 6), in which substantial growth occurs over 1979–1988. If Buckland et al.'s (1992) estimated population trajectory was an accurate assessment of the true population trend, then the results presented here suggest either 1) that the population growth rate was less than R_m=0.04; or 2) that kill was under-estimated during the 1980's for reasons discussed above; or 3) that a skewed age-structure led to a lagged response to the large decrease in kill during the 1970's; or 4) some combination of these possibilities.

Current status

Estimated kill from the fishery in recent years has been as high as 19,526, with an average kill of 13,900 from 1986 to 1990 (DeMaster et al., 1992), which represented a kill rate of 2.1% of the population estimate of 632,700. As indicated by Equation 3, the estimates of historical population size presented here, which are back-calculated from 1988, were based only on kill data through 1987. Estimated kill was 18,793 in 1988 (IATTC, 1989) and 15,245 in 1989 (Hall and Boyer, 1991), representing 3.0% and 2.4% of the abundance

[4]Gerrodette, T., and C. Perrin. 1991. Calibration of shipboard estimates of dolphin school size from aerial photographs. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-36, 24 p.

[5]Goodman, D. 1984. Consideration of age structure in back projection calculations for the northern offshore spotted dolphin population. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-84-26C, 25 p.

estimate, respectively. These recent kill estimates were the highest since 1976 (Table 2), and may have been high enough to prevent recent recovery of the population. The most recent estimates of the abundance index from tuna vessel sighting data indicated the population was declining from 1986 to 1991 (Anganuzzi et al., 1992[6]). However, the most recent kill information indicated a substantial reduction in kill to less than 1% of the population in both 1990 (5,378, Hall and Boyer, 1992) and 1991 (5,879, Hall and Lennert, in press), which resulted in an average kill per year for 1988–91 of 11,324, or 1.8% of the population estimate of 632,700. Therefore, the current status of the population is unlikely to be substantially different from what it was in 1988. Managing kill levels so that they do not exceed some fraction of the expected maximum net recruitment rate may be the most reasonable management strategy for promoting recovery of the population (DeMaster et al., 1992). The U.S. National Marine Fisheries Service has recently proposed listing the eastern spinner dolphin as depleted under the U.S. MMPA (Federal Register, 17 June 1992, 57FR27010). A separate proposal to list the eastern spinner dolphin as "threatened" under the Endangered Species Act was not warranted at this time, as the population is in no immediate danger of extinction (Federal Register, 19 October 1992, 57FR47620). Proposed international quotas on fisheries kill for each dolphin stock in the eastern tropical Pacific (IATTC, in press; MMC, 1993), if implemented, would ensure that mortality levels stayed low enough to allow recovery of the population to the OSP level.

Conclusions

Based on the best data available on abundance, kill, and population dynamics, the population size in 1988 of the eastern spinner dolphin was estimated to be below MNPL, within the range of 32% to 58% of pre-exploitation population size. Based on available life history data, the population size was estimated at 44% of pre-exploitation population size. Relative population size was estimated to be higher than Smith's (1983) estimate for 1979, but this difference was due mostly to the use of a new, better estimate of abundance, rather than to a recovery of the population between 1979 and 1988. Although there are uncertainties associated with this analysis, especially with the early kill data, the results indicated that the eastern spinner dolphin population was well below historical abundance levels in 1988. Most uncertainties appear to lead to over-estimates of relative population size, indicating the population may be at a lower level than indicated here. Calculation of confidence limits for relative population size showed that the precision of the estimates was sufficient to make a status determination except for higher values of R_m. However, higher growth rates ($R_m > 0.04$) were not supported by independent evidence available about the population trend since 1975. The results indicated that, as of 1988, the stock of eastern spinner dolphins was depleted as defined by the U.S. MMPA. The substantial fisheries kill that occurred after 1988 makes it unlikely that the population has experienced any significant recovery since then.

[6]Anganuzzi, A. A., S. T. Buckland, and K. L. Cattanach. 1992. Relative abundance of dolphins associated with tuna in the eastern Pacific Ocean: analysis of 1991 data. Paper SC/44/SM23 presented at the annual meeting of the Int. Whal. Comm.

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Spring distribution and abundance of ichthyoplankton in the tidal Delaware River

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Abstract.—Water quality in the tidal freshwaters of the Delaware River has improved substantially over the last decade. Areas near Philadelphia that were once anoxic now rarely experience dissolved oxygen concentrations lower than 3 ppm. To assess how fish spawning and nursery activity in the river has changed following these water quality improvements, ichthyoplankton were collected from April to June in 1987 and 1988 in the tidal freshwaters of the Delaware River and compared to data available from studies conducted during the mid-1970's. Eighteen taxa were collected in the present study; larval *Morone americana* (white perch), *Alosa sapidissima* (American shad), and *Alosa* spp. (river herring) were the most abundant. Total density of eggs and larvae was highest upstream of Philadelphia, where water quality has historically been highest. Ichthyoplankton density and taxonomic composition in the tributaries were similar to the most productive portions of the mainstem, except in the Schuylkill River. There, water quality is still poor, and ichthyoplankton density was an order of magnitude less than in the mainstem. In comparison to data from the previous decade, the present assemblage of the Delaware River was more diverse. Nine taxa, most notably *A. sapidissima*, were significantly more abundant in at least one portion of the river in the present study, though total ichthyoplankton density was no higher than prior to the water quality improvements. Five taxa, most notably *Cyprinus carpio* (carp), were significantly less abundant in the present assemblage.

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The tidal freshwater portion of the Delaware River was once among the most polluted estuaries in the United States. Water quality was so poor during the 1940's that gases released from the water reportedly tarnished metal and corroded engine parts of naval vessels moored near Philadelphia, PA (Albert, 1988). Conditions were poorest in the Philadelphia area, where much of the river became anoxic during warmer months. This so-called pollution block substantially reduced the upriver migration of anadromous fishes such as *A. sapidissima* and *Morone saxatilis* (striped bass) (Chittenden, 1971, 1974).

Installation of secondary treatment at municipal sewage treatment plants along the river has reduced organic loading by more than 75% since the early 1970's (Albert, 1988). As a result, dissolved oxygen concentration in the river has increased, and the magnitude and duration of the pollution block near Philadelphia has been reduced. In areas that were once anoxic, dissolved oxygen concentrations during the spring are now rarely lower than 5 ppm, or 3 ppm during the summer (Albert, 1988). Fishery resources appear to have responded to the improved water quality conditions; the size of the *A. sapidissima* spawning population has increased substantially (Maurice et al., 1987) and average catch of young-of-year *M. saxatilis* has increased by more than an order of magnitude[1].

Despite the size and importance of the Delaware estuary, little is known about which fish use the tidal freshwater region of the river as a spawning and nursery ground. The most recent regional ichthyoplankton survey was conducted in 1981, but covered 100 km of river with only 20 samples per week and only data for *M. saxatilis* were reported[2]. Numerous ichthyo-plankton collections were conducted in the mid-1970's as part of power plant or industrial-related impact studies, but these were individually limited in spatial extent and have never been integrated to provide a regional description. Most important, however, no regional study has been conducted since the dramatic improvements in water quality occurred. In this study we provide new data to describe present ichthyoplankton distribution and abundance in the tidal Delaware

[1] Weisberg, S. B., W. H. Burton, and H. A. Wilson. 1991. Delaware River striped bass studies: population estimate of the 1990 year class and an evaluation of the young-of-year index of abundance. Rep. to the Delaware Basin Fish and Wildl. Manage. Coop., Trenton, NJ.

[2] Himchak, P. J., J. Carlson, and R. Tilton. 1981. Spawning and recruitment of the striped bass, *Morone saxatilis*, in the Delaware River. Rep. available from New Jersey Dep. Environ. Protection, Trenton, NJ, Bureau of Marine Fisheries.

River and its tidal tributaries, integrate data from the many ichthyoplankton collections conducted during the 1970's, and compare these data to describe how spawning and nursery activity in the area has changed.

Methods

Ichthyoplankton samples were collected weekly from April to June in 1987 and 1988, following a stratified random design. Sampling in 1987 was conducted between Riverton, New Jersey (river kilometer [rkm] 174) and the fall line at Trenton, New Jersey (rkm 214) for nine weeks beginning on 22 April (Fig. 1). The sampling area was stratified into four 10-km regions. Each region was stratified further into three habitats: shoal (river depth of less than 8 m), channel bottom (within 1 m of the bottom in areas with an overall depth >8 m), and channel mid-water. Three randomly placed samples were collected from each habitat in each region during each week. Sampling in 1988 was conducted between Bristol, Pennsylvania (rkm 191), and Artificial Island, New Jersey (rkm 87), for eight weeks beginning on 18 April (Fig. 1). Allocation procedures in 1988 were the same as in 1987, except that the area was stratified into nine equally-sized regions, and in the channel bottom habitat, only two samples were collected.

The sampling of the river in 1987 also included tributary stations in Martin's Creek, Neshaminy Creek, Dredge Harbor, and Rancocas Creek. In 1988, tributary stations were established in the Schuylkill River, Raccoon Creek, Oldman's Creek, the Christina River, and at two stations in the Chesapeake Bay and Delaware River (C&D) Canal. Tributary stations were located approximately 1 km upstream of the confluence with the Delaware River, except for the second C&D Canal station, which was located near the Rt. 13 bridge, about 4 km from the river. One mid-water sample was collected from each tributary station each week, except for the C&D Canal stations, where both mid-water and bottom samples were taken weekly.

Samples from the bottom habitat were collected by using a 1-m diameter epibenthic ichthyoplankton sled; water column and shoal habitats were sampled using stepped oblique tows with a 0.5-m bongo net. Both types of gear were fitted with 505-μm mesh plankton nets. The volume of water that each net filtered was estimated with a General Oceanics digital flowmeter mounted at the mouth of the epibenthic sled and to one side of the bongo net. Tows were conducted against the current for five minutes at a speed of approximately 1.0 m/sec. The catch was preserved in 10% formalin, stained with rose bengal, and taken to the laboratory for analysis.

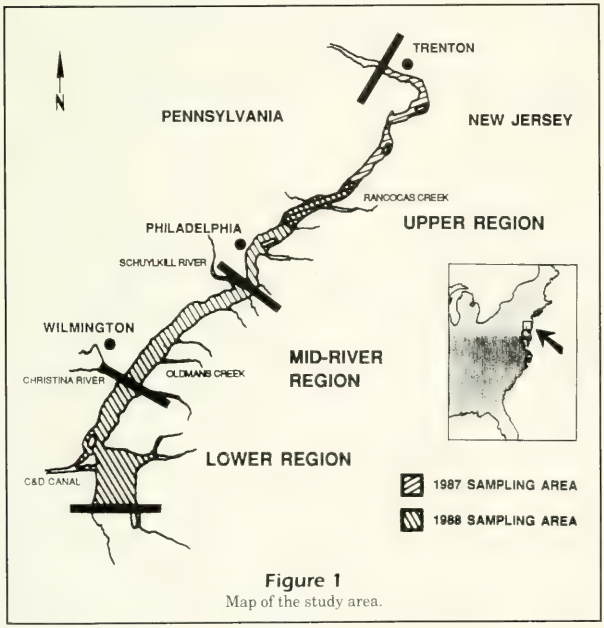

Figure 1
Map of the study area.

Physico/chemical data (temperature, dissolved oxygen, pH and conductivity) were collected weekly with a calibrated Hydrolab Surveyor II in each of the river regions, the C&D Canal, and at each of the tributary stations. Measurements in the river and in the C&D Canal were taken at surface, mid-depth, and bottom. In the tributaries, measurements were taken at surface and bottom. Water transparency was measured with a 20-cm Secchi disk.

In the laboratory, all eggs with diameters greater than 1.0 mm were removed from the collections and inspected to determine if they were *M. saxatilis* or *A. spidissima* based on the size of the perivitelline space relative to the diameter of the egg. Small eggs (less than or equal to 1.0 mm in diameter) consisted mostly of *M. americana*, *Alosa aestivalis* (blueback herring), or *Alosa pseudoharengus* (alewife), but were not differentiated quantitatively. *M. americana* yolk-sac larvae were dis-

tinguished from *M. saxatilis* larvae based on the smaller size of *M. americana* at this stage and on gut morphology, which in *M. americana* parallels the notochord for about six myomeres before turning downward. Post yolk-sac *M. americana* and *M. saxatilis* larvae less than 8 mm in length were separated by size and the formation of fin rays, (formation of fin rays occurs at about 5 mm and 8 mm, respectively). Post yolk-sac larvae of 8 mm and longer were identified by clearing and staining the specimens and examining the pterygiophore/neural spine interdigitation patterns (Olney et al., 1983). *A. sapidissima* larvae were separated from *Alosa* spp. by counting post-anal myomeres (Lippson and Moran, 1974[3]; Chambers et al., 1976).

For the purpose of data presentation, the Delaware River sampling effort was post-classified into lower river, mid-river, and upper river regions (Fig. 1). These regions corresponded to Artificial Island (rkm 87) to the Christina River (rkm 114), Christina River to the Schuylkill River (rkm 148), and Schuylkill River to Trenton, NJ (rkm 214), respectively. Density estimates were calculated for each region during each week as the simple average of all samples collected in that region. A Friedman's rank-sum test, blocked on week, was used to test for differences in density among regions (Conover, 1980).

Data from over 2,000 ichthyoplankton samples collected from the Delaware River during the 1970's were obtained from reports submitted as part of regulatory requirements or environmental impact studies (ANSP, 1974[4]; Anselmini, 1974[5]; Anselmini 1976[6]; Potter et al., 1974, a and b[7,8]; Harmon and Smith 1975[9]; PECO, 1977, a–e[10,11,12,13,14]; IA, 1979, a and b[15,16]; RMC, 1979[17]). While none of these studies individually provided coverage of the entire tidal river, collectively they provided excellent coverage. To compare present ichthyoplankton composition and abundance with that in the 1970's, these data were digitized and summarized.

To maximize comparability of data between periods, we extracted for analysis from the historical reports only those samples which were collected between mid-April and mid-June with a 500-μm mesh gear that was towed for at least five minutes and filtered at least 40 m^3. Where studies differed in taxonomic level of identification, data from all studies were restated to the higher taxonomic group. From these data, weekly average densities were estimated for each region and year. Historic abundances for each region were taken as the simple averages of weekly estimates. We included data for only years in which collections were taken in at least eight weeks between April and June to ensure that our comparison was not biased by data sets with limited temporal coverage. Comparisons of average abundance with the present study were accomplished separately for each region by using a Friedman's test blocked on week.

Results

Water quality

Water temperature during the 1987 and 1988 survey ranged from 11 to 26°C. Differences in temperature between regions were less than 1°C in both years.

[3] Lippson, A. J., and R. L. Moran. 1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Available from Maryland Department of Natural Resources. Ref. No. PPSP–MP–13, 282 p.

[4] ANSP (Academy of Natural Sciences of Philadelphia). 1974. Ecological studies in New Jersey, Oldman's Creek, Raccoon Creek, Birch Creek, and the Delaware River 1972–1973. Prep. by ANSP, Philadelphia, Pennsylvania for the Shell Oil Company, Philadelphia, PA.

[5] Anselmini, L. D. 1974. An ecological study of the Delaware River in the vicinity of the Mercer Generating Station, Trenton, NJ. Prep. by Ichthyological Associates, Inc., Ithaca, NY, for Public Service Electric and Gas Co., Newark, NJ.

[6] Anselmini, L. D. 1976. An ecological study of the Delaware River in the vicinity of Newbold Island. Prep. by Ichthyological Associates, Inc., Ithaca, NY, for Public Service Electric and Gas Co., Newark, NJ.

[7] Potter, W. A., D. C. Smith, and P. L. Harmon. 1974a. An ecological study of the Delaware River in the vicinity of Chester Generating Station. Chester Progress Rep. 1. Prep. by Ichthyological Associates, Inc., Ithaca, NY, for the Philadelphia Electric Co., Philadelphia, PA, 94 p.

[8] Potter, W. A., D. C. Smith, and P. L. Harmon. 1974b. An ecological study of the Delaware River in the vicinity of Eddystone Generating Station. Eddystone Progress Rep. 3. Prep. by Ichthyological Associates, Inc., Ithaca, NY, for the Philadelphia Electric Co., Philadelphia, PA, 42 p.

[9] Harmon, P. L., and D. C. Smith. 1975. An ecological study of the Delaware River in the vicinity of Eddystone generating station. Eddystone Progress Rep. 4 to Philadelphia Electric Co., Philadelphia, PA.

[10] PECO (Philadelphia Electric Company). 1977a. Chester Generating Station, 316(b) Rep., Permit No. PA 0011614. Rep. to the EPA, Philadelphia, PA.

[11] PECO. 1977b. Richmond Generating Station, 316(b) Rep., Permit No. PA 0011649. Rep. to the EPA, Philadelphia, PA.

[12] PECO. 1977c. Southwark Generating Station, 316(b) Rep., Permit No. POA 00116-65. Rep. to the EPA, Philadelphia, PA.

[13] PECO. 1077d. Delaware Generating Station, 316(b) Rep., Permit No. PA 0011622. Rep. to the EPA, Philadelphia, PA.

[14] PECO. 1977e. Eddystone Generating Station, 316(b) Rep., Permit No. PA 00137-14. Rep. to the EPA, Philadelphia, PA.

[15] Ichthyological Associates (IA). 1979a. Effect of the cooling water intake structure, intrainment and impingement of fishes. Burlington Generating Station Demonstration for Section 316(b) of the Federal Water Pollution Control Act Amendments of 1972, PL 95-500. Prep. by IA, Ithaca, NY, for Public Service Electric and Gas Co., Newark, NJ.

[16] Ichthyological Associates (IA). 1979b. Effect of the cooling water intake structure, intrainment and impingement of fishes. Mercer Generation Station Demonstration for Section 316(b) of the Federal Water Pollution Control Act Amendments of 1972, PL 95-500. Prep. by IA, Ithaca, NY, for Public Service Electric and Gas Co., Newark, NJ.

[17] Radiation Management Corporation (RMC). 1979. An evaluation of the cooling water intake at the Edge Moor Power Station. Edge Moor Power Station section 316(b) Evaluation. Permit No. DE-000058. Prep. by RMC, Pottstown, PA, for Delmarva Power and Light Co., Wilmington, DE.

Temperature, dissolved oxygen, and salinity were not vertically stratified in the water column and did not differ substantially between tributaries and the nearest mainstem water quality sampling locations.

Average dissolved oxygen values decreased over the sampling period during each year of the study, ranging from greater than 10 mg/L during the first week to less than 8 mg/L during the last week. Dissolved oxygen differed by as much as 3 mg/L among regions, with the lowest values occurring downstream of Philadelphia. However, only a single measurement below 5 mg/L was recorded in 1988, and no measurements below 6 mg/L were recorded in 1987.

The river was consistently fresh upstream of Pea Patch Island (km 98); salinity averaged less than 2 ppt in the regions downstream of Pea Patch Island. The highest salinity (5 ppt) was observed in the C&D Canal during the second week of sampling in 1988. A storm and subsequent freshwater runoff during the sixth week of the 1988 sampling turned the entire mainstem sampling area fresh but had little effect on salinity in the C&D Canal, which never fell below 2 ppt.

Distribution of eggs and larvae

Eighteen taxa, comprising 15 families, were collected from the Delaware River during 1987 and 1988 (Table 1). Seventeen of these taxa also were found in the tributaries (Table 2); no taxon occurred only in the tributaries. Most taxa were not abundant. Only three,

Table 1

Average density (no./100 m^3) of ichthyoplankton in the lower, mid- and upper regions of the Delaware River during the present and previous (1972–1978) studies. Values in bold represent regional densities that were significantly ($P<0.05$) different between the present and previous studies.

	Present study			Previous studies		
	Lower river	Mid river	Upper river	Lower river	Mid river	Upper river
Percichthyidae						
Morone saxatilis (eggs)	0.2	0.2	<0.1	0.1	0.3	0
Morone saxatilis	0.1	**0.4**	0.1	0.3	0.1	0
Morone americana	0.5	**8.4**	48.3	1.1	0.4	27.2
Clupeidae						
Alosa sapidissima (eggs)	0.1	**0.1**	**0.4**	0	0	0.1
Alosa sapidissima	**0.8**	**15.0**	**49.0**	0	0	0
Other Alosa spp.	0.2	5.4	33.5	**4.1**	22.8	**339.7**
Brevoortia tyrannus	**0.1**	0.1	0	0	0	0
Dorosoma cepedianum	0	0	0	0	<0.1	0
Ictaluridae	0	0	0.1	0	0	0
Anguillidae						
Anguilla rostrata	<0.1	<0.1	<0.1	**0.8**	**0.4**	**0.2**
Percidae						
Perca flavescens	<0.1	0	**0.7**	0	0	<0.1
Etheostoma sp.	<0.1	<0.1	0.2	0	0	0.6
Cyprinidae	0.1	1.3	0.5	**1.0**	**6.8**	**10.5**
Soleidae						
Trinectes maculatus	**0.1**	**0.1**	<0.1	0	0	0
Centrarchidae						
Lepomis sp.	<0.1	<0.1	**0.1**	0	0	0
Pomoxis sp.	0	0	0	0.1	0	<0.1
Catostomidae						
Carpiodes cyprinus	<0.1	**0.4**	0.6	0	0	**3.4**
Castostomus sp.	0	0	0	0	0	**1.0**
Engraulidae						
Anchoa mitchilli	0.6	0.1	<0.1	0.2	0	0
Gasterosteidae	<0.1	<0.1	<0.1	0	0	0
Cyprinodontidae						
Fundulus sp.	0	0	<0.1	00.1	<0.1	
Sciaenidae						
Leiostomus xanthurus	**0.5**	**0.1**	<0.1	<0.1	0	0
Atherinidae						
Menidia sp.	0.2	<0.1	<0.1	0.4	0	0
Umbridae						
Umbra pygmaea	0	0	0	0	0	<0.1

Table 2

Average density (no./100 m^3) of ichthyoplankton in the Delaware River tributaries among samples collected in 1987 and 1988.

	C&D Canal	Christina River	Oldman's Creek	Raccoon Creek	Schuylkill River	Dredge Harbor	Rancocas Creek	Neshaminy Creek	Martin's Creek
Percichthyidae									
Morone saxatilis (eggs)	5.7	0.2	0	0.2	0	0	0	0	0
Morone saxatilis	0	0	0.7	1.5	0	0	0	0	0
Morone americana	0.1	21.5	8.0	30.9	1.4	4.0	36.9	8.8	2.4
Clupeidae									
Alosa sapidissima (eggs)	<0.1	0	0	0	0	0	1.6	0	0
Alosa sapidissima	0	41.4	168.4	247.3	1.3	80.7	199.9	46.6	75.5
Other *Alosa* spp.	0	28.6	106.4	160.6	1.0	52.0	194.5	52.7	57.8
Anguillidae									
Anguilla rostrata	0	0	0	0	0	0	0	0.1	0
Percidae									
Perca flavescens	<0.1	1.0	0	0	0	0	1.3	0	0
Etheostoma sp.	<0.1	2.2	0.2	0.1	0	0	0.1	0.1	0
Cyprinidae	0	0.6	0.8	7.4	0.6	0	<0.1	2.1	0
Soleidae									
Trinectes maculatus	0.1	0	0	0	0	0	0	0	0
Centrarchidae									
Lepomis sp.	0	0	0	0.4	0	0.3	0.6	0.4	0.5
Catostomidae									
Carpiodes cyprinus	0	2.8	0.2	0.8	0	0.1	0.7	0.2	0
Engraulidae									
Anchoa mitchilli	0.1	0	0	0	0	0	0	0	0
Gasterosteidae	0.1	0	0	0	0	0	0	0	0
Cyprinodontidae									
Fundulus sp.	0	0	0	0	0	0	<0.1	0	0
Sciaenidae									
Leiostomus xanthurus	1.8	0	0	0	0	0	0	0	0
Atherinidae									
Menidia sp.	0.1	0	0	0	0	0	0	0	0

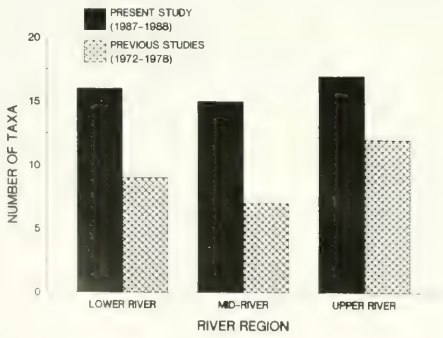

Figure 2

Number of ichthyoplankton taxa found in each of the three regions of the tidal Delaware River in the present (1987–1988) and in previous (1972–1978) studies.

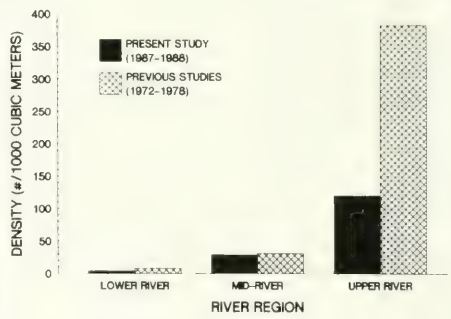

Figure 3

Average ichthyoplankton density (#/1000 m^3) in each of the three regions of the tidal Delaware River in the present (1987–1988) and in previous (1972–1978) studies.

A. sapadissima, *M. americana*, and *Alosa* spp., occurred at average densities greater than 10/100 m^3 in either the mainstem or the tributaries.

Numbers of taxa did not differ significantly among the three regions of the river (Fig. 2), but average ichthyoplankton density did ($P<0.001$) (Fig. 3). Density was greatest in the upper region (between the Schuylkill River and Trenton, NJ) where it averaged more than 120 larvae/100 m^3 during the study. In contrast, density in the mid-river region (between Phila-

Table 3

Comparison of highest weekly ichthyoplankton density (no./100 m^3) found in the lower, mid, and upper river sampling regions between the 1987–1988 study and historical studies.

	Present study			Historical studies				
	Lower river	Mid river	Upper river	Lower river	Mid river		Upper river	
	(1988)	(1988)	(1987–1988)	(1978)	(1974)	(1977)	(1972)	(1973)
Percichthyidae								
Morone saxatilis (eggs)	0.6	0.6	0.1	0.3	0	2.9	0	0
Morone saxatilis	0.2	2.5	1.2	1.1	0	0.7	0	0
Morone americana	1.7	31.2	387.2	2.7	2.0	2.5	56.1	125.0
Clupeidae								
Alosa sapidissima (eggs)	0.2	0.4	1.4	0	0	0	1.7	0
Alosa sapidissima	3.5	52.0	219.6	0	0	0	0	0
Other *Alosa* spp.	0.9	26.8	151.9	14.5	202.5	51.3	3231.3	522.9
Brevoortia tyrannus	0.6	0.4	0	0	0	0	0	0
Dorosoma cepedianum	0	0	0	0	0	0.2	0	0
Ictaluridae	0	0	0.8	0	0	0	0	0
Anguilla rostrata	0.1	0.1	0.1	3.7	0.2	0.6	0.5	0
Percidae								
Perca flavescens	0.1	0	3.6	0	0	0	0.3	0.2
Etheostoma sp.	0	0.1	1.1	0	0	0	5.4	1.6
Cyprinidae	0.4	9.1	5.8	4.2	51.8	45.6	84.5	24.6
Soleidae								
Trinectes maculatus	0.4	0.2	0.1	0	0	0	0	0
Centrarchidae								
Lepomis sp.	0.1	0.3	0.3	0	0	0	0	0
Pomoxis sp.	0	0	0	0	0	0	0	0
Catostomidae								
Carpiodes cyprinus	0.3	3.3	2.1	0	0	0	26.4	0.7
Catostomus sp.	0	0	0	0	0	0	24.4	1.8
Engraulidae								
Anchoa mitchilli	1.8	1.1	0.4	0.7	0	0	0	0
Gasterosteidae	<0.1	0.2	<0.1	0	0	0	0	0
Cyprinodontidae								
Fundulus sp.	0	0	0.1	0	0.4	0	0	0
Sciaenidae								
Leiostomus xanthurus	1.8	0.2	<0.1	0	0	0	0	
Atherinidae								
Menidia sp.	0.5	0.1	<0.1	1.8	0	0	0	0
Umbridae								
Umbra pygmaea	0	0	0	0	0	0	0.3	0

delphia, PA and Wilmington, DE) was only about one-fourth of that in the upstream area. Average larval density in the lower region (downstream of Wilmington) was less than 4/100 m^3 and never exceeded 10/100 m^3 during any week of the study (Table 3).

Species composition was fairly consistent between the mid- and upper regions but differed substantially in the lower river region (Table 1). *M. americana, A. sapidissima*, and *Alosa* spp. were dominant in the upper river, occurring at densities of an order of magnitude greater than any other taxa. In the region furthest downstream, where salt intrusion begins to occur, species typical of the estuarine environment, such as *Leiostomus xanthurus* (spot) and *Anchoa mitchilli* (bay anchovies), were at least as abundant as *A. sapidissima* and *Alosa* spp. Freshwater species that occurred in the upper river, such as *Etheostoma* sp. (darters) and *Ictaluridae* (catfish), were not found in the more saline region.

With the exception of the Schuylkill River and the C&D Canal, density and taxonomic composition in the tributaries was similar to that in the most upstream region of the tidal mainstem (Table 2). The Schuylkill River is the largest tributary to the Delaware River and flows through a heavily industrialized portion of Philadelphia. Only four taxa were collected there, and they generally occurred at densities 10- to 100-fold lower than in any other tributary. No species occurred

there at a density greater than 10/100 m^3. The other anomalous tributary was the C&D Canal, which is not a true tributary, but a man-made, free-flowing canal constructed in the early 1900's to link the Delaware and Chesapeake estuaries for navigation. The C&D Canal contains virtually no freshwater drainage, and the species composition there was most similar to the lower region of the mainstem. No clupeid larvae and very few *M. americana* larvae were collected there, but the C&D Canal did contain densities of *M. saxatilis* eggs considerably higher ($P<0.01$) than the mainstem or other tributaries.

Potential bias in the recent survey could exist because sampling in the upper river region was primarily accomplished in 1987, whereas the downstream areas were sampled in 1988. To determine if this was a problem, we compared ichthyoplankton density and species composition in the area sampled in common between the two years. We found that the difference in total ichthyoplankton density between the two years was less than 10% (Table 4) and not significantly different. In addition, none of the dominant taxa had more than a two-fold difference in density between years. Temporal patterns for the dominant taxa were generally consistent across both years of the study (Fig. 4). Seasonal peaks in larval abundance for *Perca flavescens* (yellow perch) preceded that of the *Alosa* spp., followed by *M. americana* and *M. saxatilis*. *A. sapidissima* and *P. flavescens* larval abundance peaked about a week later in 1988 than in 1987. This difference may be attributable to inter-annual variability in spawning peaks; however, since sampling in 1988 was concentrated farther downriver, the difference in temporal patterns between years may partly reflect the time required for downstream transport of larvae from upstream spawning grounds.

Comparison with historical data

When we compared our data to the historic data, we found that average density of all eggs and larvae did not differ significantly in the two lower regions and that historical density was higher ($P<0.01$) in the most upstream region (Fig. 3). The larger difference among periods was in composition and dominance; the number of taxa caught in each region in the present study was almost double that in the historical data (Fig. 2), despite the greater number of sampling years encompassed by the previous studies. Whereas river herring accounted for more than half of the catch in every region during the 1970's, no taxon accounted for more than 40% of total catch in any region in the present study (Table 1).

Density of nine taxa increased significantly in at least one region since the previous decade (Table 1). Of these, the increase was most dramatic for *A. sapidissima*. In the earlier studies, *A. sapidissima* eggs were rarely found, and larvae were not encountered at all. In contrast, the density of shad larvae in the upper river region exceeded 100/100 m^3 during several weeks of our study (Table 3). Five taxa decreased significantly in number in at least one region, and cyprinids (minnows) and *Anguilla rostrata* (elvers) declined significantly in all three regions. Cyprinids were only about one-tenth as abundant in our study. Although we did not identify all of the cyprinids in our study, the cyprinids collected consisted primarily of juvenile *Notropis* spp., whereas most cyprinids in previous studies were identified as juvenile *C. carpio*.

Table 4

Average ichthyoplankton density (no./100m^3) in the area and weeks samples in common between 1987 and 1988.

	1987	1988
Percichthyidae		
Morone saxatilis (eggs)	0	<0.1
Morone saxatilis	0	0.1
Morone americana	23.7	38.4
Clupeidae		
Alosa sapidissima (eggs)	1.2	0.8
Alosa sapidissima	40.2	65.0
Other *Alosa* spp.	31.4	21.0
Anguillidae		
Anguilla rostrata	<0.1	0
Percidae		
Perca flavescens	1.7	0.5
Etheostoma sp.	0.2	1.0
Cyprinidae	0.1	0.4
Soleidae		
Trinectes maculatus	0	<0.1
Catostomidae		
Carpiodes cyprinus	1.1	0.2
Sciaenidae		
Leiostomus xanthurus	0	<0.1
Gasterosteidae	0	<0.1

Discussion

The dramatic decline of *A. sapadissima* productivity in the Delaware River since the last century (Chittenden, 1974) has been attributed to reductions in the amount of usable spawning habitat (Chittenden, 1976). Shad have historically used all of the Delaware River as spawning and nursery grounds, but spawning during most of this century was limited to areas 200-km upstream from the tidal freshwater areas we studied. Size of the spawning ground was reduced for two reasons (Chittenden, 1976). First, only the earliest arriving shad, which typically spawn farthest up-

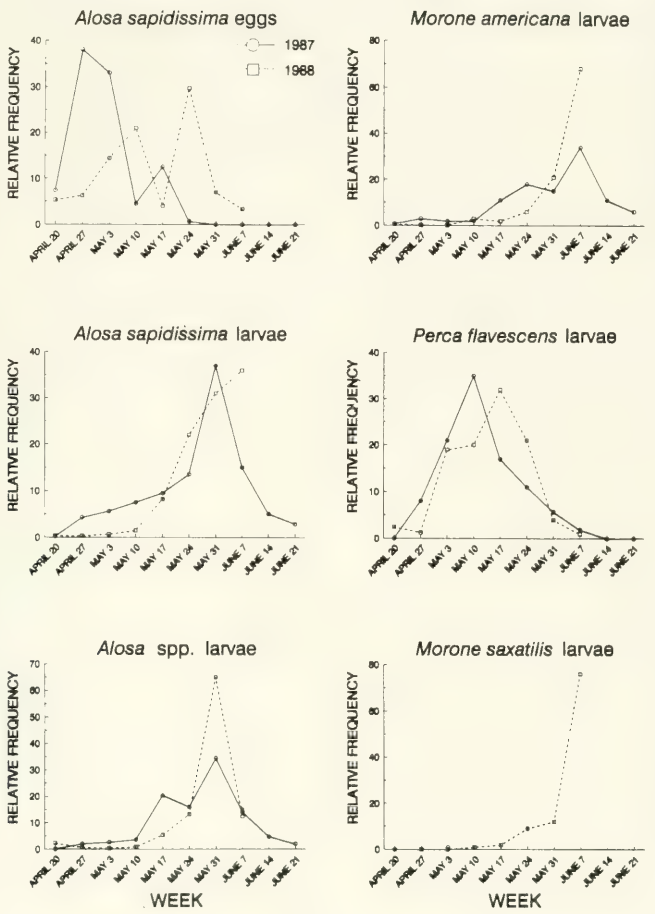

Figure 4

Temporal patterns of abundance for the dominant larval fish of the tidal Delaware River. Solid and dashed lines represent 1987 and 1988, respectively.

stream (Glebe and Leggett, 1981; Maurice et al., 1987), could get past Philadelphia before hypoxic conditions developed. Second, only fish migrating out of the river late in the season, that is fish spawned in the most upstream reaches, arrived in the Philadelphia area after the lethal dissolved oxygen conditions dissipated.

Our data suggest that the spatial extent of *A. sapidissima* spawning habitat in the Delaware River has expanded over the last decade, coincident with the water quality improvements near Philadelphia. While we found no evidence of spawning or nursery activity in tidal freshwater during the 1970's, prior to water quality improvements, by the late 1980's the density of larvae there was as high as in non-tidal upstream reaches. The suggestion of expanded spawning ground for shad is consistent with Maurice et al. (1987), who documented substantial increases in spawning activity during the last decade in the lower reaches of the

non-tidal river. Presumably, expansion of the spawning and nursery grounds is a first step in recovery of the stock.

There was little difference in *M. americana* abundance in the Delaware River between our study and the historical data (Tables 1 and 3), suggesting that the poor water quality may have had little impact on *M. americana* spawning and nursery activities in the Delaware River. We observed that most *M. americana* larvae were concentrated upstream of Philadelphia in an area where water quality was not as seriously impacted as below Philadelphia (Albert, 1988). Unlike *A. sapidissima*, which leave the estuary and must return through the Philadelphia region to spawn, *M. americana* remain in the estuary throughout their life cycle. Presumably, these life history characteristics have allowed *M. americana* to avoid effects of the poor water quality of the Philadelphia area more effectively than shad.

We found that larval *M. saxatilis* were primarily concentrated in the area downstream of Philadelphia. Since this area historically had the worst water quality, the *M. saxatilis* population should have benefitted from water quality improvements. The Delaware River beach seine monitoring survey, conducted annually by the State of New Jersey, showed a consistent increase in young-of-year *M. saxatilis* abundance throughout the 1980's[1]. However, we did not find the density of eggs to be higher in our study than in the 1970's, and the density of larvae was only slightly higher. We did find that present densities of *M. saxatilis* eggs and larvae in the Delaware River are considerably less than in the Hudson River[18] or the Chesapeake Bay (Setzler-Hamilton et al., 1981; Grant and Olney, 1991). This may be due, in part, to a year effect, since juvenile abundance in the Delaware River in 1988, as measured by the beach seine survey, was lower than in any other year since 1985. However, it is possible that higher juvenile abundance in the late 1980's resulted from better survival of larvae as water quality improved (Burton et al., 1992), rather than from increased egg production.

We found that the density of *M. saxatilis* eggs was considerably higher in the C&D Canal than in the mainstem Delaware River. This finding seems to support studies suggesting that the mechanism for maintenance of the Delaware River *M. saxatilis* population is transport of eggs spawned in the Chesapeake Bay through the C&D Canal (Chittenden, 1971; Johnson and Koo, 1975). Our data, however, are probably more consistent with that of Kernehan et al. (1981), who suggested that most of the eggs transported through the canal are not viable. In spite of finding considerably elevated densities of eggs in the C&D Canal, no larvae were found there, and we collected fewer than 10 larvae within 10 km of where the C&D Canal empties into the Delaware River estuary. Most of the *M. saxatilis* larvae we found in the Delaware River were collected between the Delaware Memorial (rkm 111) and Commodore Barry (rkm 132) bridges, more than 30 km upstream of the C&D Canal. This distance represents about three tidal excursion distances, and while upstream transport of eggs is possible in some estuarine systems (Norcross and Shaw, 1984), it is unlikely to occur in this portion of the Delaware because of the lack of a well-defined thermocline or pycnocline that would allow for two-layer circulation. Thus, it is more likely that most of the *M. saxatilis* larvae found in the Delaware River were actually spawned in the river.

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Acknowledgments

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Effects of entanglement and escape from high-seas driftnets on rates of natural mortality of North Pacific albacore, *Thunnus alalunga*

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North Pacific albacore (*Thunnus alalunga*) are heavily fished and may have experienced recent reductions in recruitment (NOAA, 1991). U.S. troll fishery landings and catch per unit of effort (CPUE) have been decreasing since the 1960's and are currently at only about 50% of their peak levels (Kleiber and Perrin, 1991; NOAA, 1991). Landings and CPUE by the Japanese pole-and-line fishery have also been falling continuously since the late 1970's[1]. North Pacific albacore are additionally targeted by longline fleets, and considerable numbers are taken by high-seas large- and small-mesh driftnet fleets. The small-mesh fleets of Japan, Taiwan, and Korea target neon flying squid (*Ommastrephes bartramii*) and incidentally capture albacore. The large-mesh fleets of Japan and Taiwan target albacore, skipjack tuna (*Katsuwonus pelamis*), and various billfishes (*Istiophoridae* and *Xiphiidae*).

Foreign driftnet fleets and U.S. trollers taking albacore overlap geographically (Fig. 1). They also target a common stock even when fishing in widely separated areas because of the trans-Pacific migration of albacore (Otsu and Uchida, 1963). Albacore that encounter drift nets, and escape to survive long enough to be recaptured by another fishery can bear some external marks[2,3]. These marks provide direct evidence of interactions among fisheries. U.S. trollers operating in the North Pacific have reported an increased frequency of net-marked fish with the expansion of the Taiwanese, Korean, and Japanese high-seas driftnet fleets (NOAA, 1991;[2,3]).

Albacore that become entangled in drift nets face a number of possible fates (Fig. 2). The fraction that become entangled and subsequently drop out (alive or dead) is not known. If it is significant, the North Pacific albacore stock could be affected more seriously by high-seas drift nets than landings alone indicate. Our study, part of a larger effort to determine the impacts of drift nets on the North Pacific albacore stock, was undertaken to determine whether albacore that encounter drift nets, and subsequently escape alive, suffer higher than normal rates of natural mortality.

Our strategy was to look for differences in measures of fitness, and differences in short-term and long-term growth rates between net-marked (i.e., fish that have encountered drift nets and escaped) and unmarked albacore. We also looked for indications of bacterial infection and long-term stress in net-marked albacore. These parameters could evince, although not quantify, differences in rates of natural mortality. We had to use indirect measures because rates of natural mortality (or physiological changes) could not be directly observed in albacore encountering simulated drift nets in shoreside tanks. Unlike skipjack and yellowfin tuna (*Thunnus albacares*) (Brill, 1992), albacore have yet to be successfully maintained in captivity.

Selection of specific parameters was constrained by the necessity of collecting measurements and samples at sea aboard small commercial fishing vessels. We could acquire only measurements and samples that could be obtained under difficult conditions and that did not interfere with normal fishing operations. We were further limited to collecting samples that could be stored for later processing in the laboratory and that would not reduce the market value of the catch. Given these constraints, we chose the following parameters. Weight to length and maximum girth to length ratios were used as indicators of general fitness (Bolger and

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[2]Bartoo, N., D. B. Holts, and C. Brown. 1991. Report of the 1990 cooperative albacore observer project. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., NOAA, Southwest Fish. Sci. Cent., B.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-09, 16 p.

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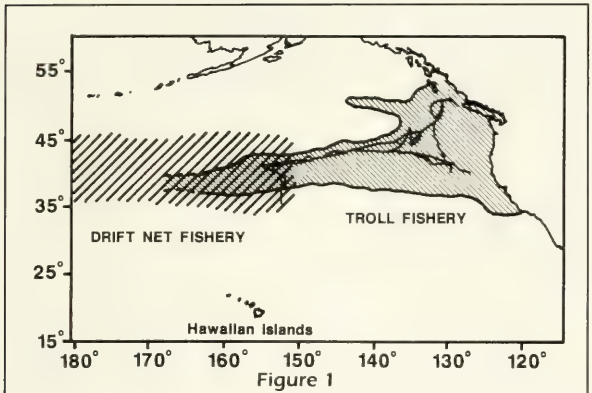

Figure 1

Area of operation of the U.S. troll fishery (light cross-hatching) catching albacore. Track lines of U.S. vessels carrying National Marine Fisheries Service observers in 1991 are shown by the solid line. Area of operation of foreign drift net fleets (heavy cross-hatching) extends west to approximately 140°W.

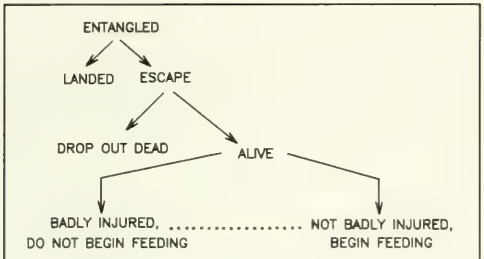

Figure 2

The possible fates of albacore that become entangled in high-seas drift nets. Note that the condition of fish which escape drift nets alive probably form a continuum from those that are so badly injured that they succumb quickly, to those that are only slightly injured and resume feeding immediately.

Connolly, 1989; Cone, 1989, 1990; Murphy et al., 1991). Relative otolith weight (i.e., the ratio of otolith weight to body weight) was used as an indicator of long-term growth rate (Boehlert, 1985; Pawson, 1990; Fletcher, 1991). (Because otolith weight is proportional to fish age rather than to body size, slower-growing fish have larger otoliths at a given body size because they have taken longer to reach that body size.) RNA:DNA ratio of white muscle was measured because it is an established indicator of short-term (days to weeks) growth rates (Bulow, 1970; Bulow et al., 1981; Ferguson and Danzmann, 1990; Mustafa et al., 1991). Relative leukocyte abundance (i.e., the ratio of leukocytes to red blood cells) was assessed as an indicator of bacterial infection and long term stress (Blaxhall, 1972; Anderson, 1990; Goede and Barton, 1990). Although muscle lipid content can be used as a measure of recent feeding history (Dotson, 1978), it was not used in this study. The lipid content of tuna muscle is dependent on sampling site (Dotson, 1978; Vileg et al., 1983; Boggs and Kitchell, 1991) and this factor could not be rigorously controlled.

Materials and methods

During 1990 and 1991, observers were placed aboard ten U.S. trollers by the Southwest Fisheries Science Center (NMFS, NOAA), in cooperation with the Western Fishboat Owners Association. Observers documented the number of net-marked albacore landed and collected data and samples for our study. Boats operated in an area of the North Pacific shown in Figure 1. Albacore were classified according to the severity of net damage with a scheme (Table 1) developed by Bartoo et al.[2]. Fork length, maximum girth (both to the nearest centimeter), and body weight (to the nearest kilogram) were measured. Dried blood smears, sagittae (otoliths), and white-muscle samples (frozen in sealed tubes in the boats' commercial fish freezers) were also obtained from a subsample of landed fish selected by the observers. Muscle samples (taken from the small amount of muscle remaining near the skull following decapitation) and otoliths could be obtained only on vessels that processed (i.e., "gilled and gutted") their catches. Complete sets of samples were not, therefore, obtained from every fish.

In the laboratory, otoliths were dried, cleaned, and weighed to the nearest 0.1 mg on a Sartorius 1207 MP2 electronic balance. RNA and DNA were extracted from the frozen muscle samples by standard procedures (Hutchison and Munro, 1961; Munro and Fleck, 1966; Wilder and Stanley, 1983). The only modifications were that the RNA was extracted with 1.0 N NaOH, and the DNA with 1.2 N perchloric acid, both at 37°C for 60 minutes. RNA, DNA, and protein concentrations were measured with a Beckman model 35 UV spectrophotometer using the dual wave length method (Tsanev and Markov, 1960) and standard extinction coefficients (Wilder and Stanley, 1983). Red cells and leukocytes were counted in Geimsa-stained blood smears with the aid of light microscopy (oil immersion lens) in a minimum of three microscope fields, or until at least 200 red cells were counted. Eosinophils could be easily differentiated from the remainder

Table 1

Net damage classification scheme (Bartoo et al.[2]) used to assess severity of injury to albacore caused by entanglement and escape from drift nets, and the number fish in each damage code category examined for our study.

Damage code	Damage description	Number of fish
0	No damage or scarring.	217
1	Minor damage along side(s) of fish, pattern of stripes due to minor scale loss where fish forced its way through or along the net.	39
2	Minor damage to head, chiefly forward of pectoral fins, brush-like pattern of scale loss.	5
3	Severe damage from bruising or scraping away of parts of the skin, primarily in area of greatest girth and mostly on dorsal surface.	10
4	Damage of any degree that was partially or completely healed.	60

of the leukocyte population and were excluded from the total leukocyte count. Although Alexander et al. (1980) described the distinguishing features of albacore blood cells, we were only able to differentiate eosinophils clearly from the remainder of the leukocytes. Leukocytes were, therefore, not further classified.

By using data from unmarked fish only, regressions of body weight on fork length, maximum girth on fork length, and otolith weight on body weight were fitted by a least squares procedure (Statgraf Statistical Software) to the exponential equation:

$$Y = a \cdot x^b.$$

Regression parameters a and b were estimated for each case.

Relative condition factor, relative girth, and relative otolith weight for individual fish were then calculated with the regression parameters:

$$K = W/(a \cdot X^n).$$

When K = relative condition factor, W = body weight and X = fork length; when K = relative girth, W = maximum girth and X = fork length; and when K = relative otolith weight, W = otolith weight and X = body weight.

Relative condition factor, relative girth, and relative otolith weight were calculated to permit direct comparison of groups containing individuals of different body sizes (Pollard, 1972; Brill et al., 1987).

The standard condition factor (C) was calculated separately for unmarked and net-marked fish:

$$C = W / FL^3$$

where W = body weight and FL = fork length.

Fish were grouped only as net-marked (damage codes 1-4, Table 1) and unmarked (damage code 0). Differences in mean values for unmarked and net-marked fish were evaluated by unpaired Student's t-tests with $P < 0.05$ taken as the maximum level for statistical significance.

Results and discussion

The only significant differences between net-marked and unmarked fish were in measures of absolute size (mean fork length, body weight, and maximum girth), which were greater for unmarked albacore (Table 2). These data suggest that smaller fish escape drift nets, survive, and are recaptured by the troll fleet more frequently than large fish. This appears to be confirmed by size-frequency distributions for the 217 net-marked and 114 unmarked fish included in this study (Fig. 3A). The two peaks in Figure 3A (at approximately 65 and 80 cm) represent 3- and 4-year-old fish, respectively[2] and imply that 4-year-old individuals predominate the unmarked group. In the net-marked group, 3- and 4-year-old fish are approximately equally represented. This result is, however, more likely due to either a sampling bias of the observers when choosing fish for inclusion in this study, or to time-area variations in fish size composition and the percentage of net-marked fish. The size-frequency distributions of

Table 2

Parameters measured to evaluate the effects of escapement from drift nets on the natural mortality of albacore *Thunnus alalunga*. *N* equals the number of observations.

	Unmarked fish		Net-marked fish	
Parameters	Mean ± SD	*N*	Mean ± SD	*N*
Body weight* (kg)	10.6 ± 2.4	182	8.6 ± 2.6	83
Fork length* (cm)	79.1 ± 7.4	215	73.5 ± 7.9	114
Maximum girth* (cm)	56.1 ± 5.7	214	51.8 ± 6.2	113
Condition factor (kg/cm^3)	0.0208 ± 0.0015	182	0.0210 ± 0.0017	83
Relative girth	1.00 ± 0.02	214	1.00 ± 0.03	113
Relative condition factor	1.00 ± 0.07	182	1.00 ± 0.07	83
RNA to DNA ratio	6.99 ± 0.97	34	6.90 ± 1.49	36
Relative otolith weight	1.00 ± 0.09	175	0.99 ± 0.11	47
Leukocytes/200 red cells	7.26 ± 5.30	15	6.44 ± 3.59	35

*$P \leq 0.05$.

a much larger number of albacore (12,085 unmarked and 381 net-marked individuals[4]; and from which the fish used in this study are a subsample, show that the frequency distributions of 3- and 4-year-old net-marked and unmarked fish are more nearly identical (Fig. 3B); 3-year-old fish were found to be only slightly dominant in both groups.

Our objective in calculating condition factor, relative girth, and relative condition factor (also referred to as relative weight) was to determine if there was any indication of differences in fitness between unmarked and net-marked fish. No differences were found (Table 2). The use and misuse of condition factor and relative condition factor have received much recent attention (Bolger and Connolly, 1989; Cone, 1989; Murphy et al., 1991). The use of such indices in groups of fishes with different mean lengths and size-frequency distributions may not be justified because disparities may be due to differences in body size, rather than to physiological fitness (Cone, 1989, 1990). Because indices of fitness were not different for unmarked and net-marked fish, we considered the question of suitability moot.

No differences were found either in measures of short-term (RNA:DNA ratio) or long-term (relative otolith weight) growth rates (Table 2). The RNA:DNA ratio can be affected by the age of the fish (Haines, 1973); however, it was not corrected for body size (i.e., age) because we found no correlation between it and body weight.

The relative leukocyte counts also did not differ between unmarked and net-marked albacore (Table 2). We assumed that net-marked albacore could show either elevated or reduced leukocyte counts. Acute bacterial infection has been shown to increase leukocyte counts in fish (Wedemeyer et al., 1990). Conversely, reduced leukocyte counts can be caused by elevated circulating corticosteroid levels (an acute stress response) or by chronic bacterial infection causing leukocytolysis (Shreck, 1981; Wedemeyer et al., 1983). The lack of difference between unmarked and net-marked albacore suggests that none of the processes that can affect relative leukocyte counts was occurring in the latter.

We were hampered in interpreting our results because we could not determine precisely how long the fish were at liberty following escapement from drift nets. Based on observations of skipjack and yellowfin tuna held in shoreside tanks at the Kewalo Research Facility (described in Brill, 1992), skin damage resulting from capture generally heals completely within weeks in feeding fish (R. W. Brill, unpubl. observations). Fish with damage codes 1–3 (Table 1), therefore, probably encountered drift nets within one month of recapture. It was impossible to estimate how long fish with damage code 4 had been at liberty or how long net damage remains visible, although Bartoo et al.[2] speculated that fish with damage code 4 may have been at liberty more than a year since encountering a

[4]N. Bartoo, D. Holts, C. Brown, and L. Halko. La Jolla Laboratory, Southwest Fish. Sci. Cent., unpubl. data.

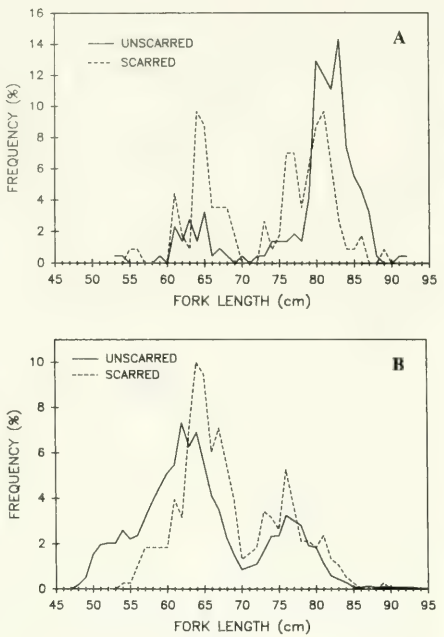

Figure 3

Size-frequency distribution of the unmarked and net-marked albacore sampled for our study (**A**) (215 unmarked and 114 net-marked fish) and much larger data set (**B**) (12085 unmarked and 318 net-marked fish) from which the fish used in our study are a subset (N. Bartoo, D. Holts, C. Brown, and L. Halko, SWFSC, La Jolla Laboratory, unpubl. data).

drift net. It is unknown if this is sufficient time for differences in relative otolith weight to become measurable. Boggs and Kitchell (1991) showed that significant weight loss occurs in tunas within one week of starvation. Therefore, it was likely that net-marked fish were at liberty long enough for measures of physiological fitness to become apparent, assuming net-marked albacore had not been feeding prior to recapture. The rate at which relative leukocyte abundance changes in albacore following stress or infection is not known, but in coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*O. mykiss*) leukocyte abundance changes within 96 hours of imposition of stressful conditions (McLeay and Gordon, 1977). Leukocyte abundance should be a good measure of differences in the health of net-marked and unmarked albacore, but the large standard deviation (Table 2) may limit its usefulness in this species.

Failure to detect differences (Table 2) between unmarked and net-marked albacore suggests that the fish escaping from drift nets, and living long enough to become vulnerable to recapture by U.S. trollers, do not suffer increased natural mortality. Most of the fish however, recaptured by trollers are found to be only minimally damaged or to have healed scars (Table 1), which may explain the lack of differences between net-marked and unmarked fish. As shown in Figure 2, there is most likely a spectrum of damage caused during encounters with drift nets. We do not know if the distribution of damage severity in the population of albacore vulnerable to the troll fishery is the same as that of all the albacore that escape drift nets alive. Also, the number of albacore falling out dead, or escaping so badly injured that they succumb before becoming vulnerable to recapture by troll vessels, may well be significant but remains to be determined.

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Weight change of pink shrimp, *Pandalus jordani*, after commercial harvest and handling

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The northeast Pacific trawl fishery for pink shrimp, *Pandalus jordani*, is unusual in that it is primarily managed by an aggregate size limit. Vessels are required to land catches with a minimum average size of 353 shrimp per kg (160 shrimp per lb). The regulation is intended to limit fishing mortality on age-one shrimp, and also to maintain the economic value of the catch (PFMC, 1981). The decision to retain shrimp from a particular tow is made by fishermen at sea; however, the regulation is enforced when the shrimp are landed in port, up to five days later. In general, a knowledge of how commercial fishing practices can influence the average weight of target species is important for effective management by an aggregate size limit (Kirkley and DuPaul, 1989). Accordingly, the objective of this study was to quantify changes in the average weight of pink shrimp from initial retention to shoreside delivery, using normal commercial handling and icing procedures.

Methods

To assess the weight change of shrimp from commercial handling practices, we compared the weight of shrimp samples taken directly from the trawl nets of commercial vessels at sea to the weight of the same samples during the subsequent shoreside delivery. Four to eight replicate samples of approximately 500g were collected from each tow and weighed to the nearest 0.1g with a magnetically dampened triple beam balance. The accuracy of the scale was checked by using a known weight prior to each trip and again prior to weighing the samples at the dock. The scale used had also been previously tested for accuracy at sea with blind weighings and had been shown to produce measurements with a coefficient of variation of less than 0.5% under a variety of sea conditions[1]. Each sample was placed in a 5-mm mesh bag, labeled and passed to a crew member. Shrimp were taken directly from the vessel's hopper and were not washed prior to weighing and bagging. The crew was instructed to distribute the sample bags throughout the other shrimp from the same tow. After placement of the samples, the crew shoveled and raked flake ice into the layers of shrimp, according to that vessel's normal procedures.

At the completion of the fishing trip, the bags were retrieved during unloading and inspected for punctures. Punctured bags were discarded. Each intact sample was opened, placed in a tub with a 7-mm mesh bottom to drain for one minute, and weighed again with the same scale. An estimate of the percentage of ice in the gross load was obtained from processing plant records.

Weight change was expressed as a percentage of the original sample weight. The average percent weight change for all samples combined, for each trip and for each day of fishing, was compared to a hypothetical weight loss of zero percent by using a one sample *t*-test. To facilitate comparisons of weight change between trips or between individual days of fishing, 95% confidence intervals were constructed for each estimate of average weight loss. Scatter plots of percent weight change for individual samples versus elapsed time were constructed for each trip and for all trips combined. Each graph was tested for a significant slope with simple linear regression.

Results and discussion

Seven sampling trips were completed aboard commercial shrimp vessels between April and August 1988, lasting from 1 to 5 days. We recovered 70% of the mesh bags intact, resulting in weight change estimates for 713 samples from 132 tows. Elapsed time from catch to unloading ranged from 4 to 121 hours.

Percent weight change for the combined samples showed an approximately normal distribution centered on a mean weight loss of 2.2%, with a 99% confidence inter-

[1] M. Saelens and R. W. Hannah. 1988. Oregon. Dep. of Fish and Wildlife, Newport, OR 97365. Unpub. data.

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Fishery Bulletin, U.S. 91:804–807 (1993).

Table 1

Mean percent weight change, standard error of the mean and number of days on ice, between capture and unloading, for 500-g samples of pink shrimp, *Pandalus jordani* (number of samples is in parentheses). Asterisks denote results significantly different from zero percent weight change.

Trip	Days on ice					All days combined
	1	2	3	4	5	
1	−1.2 ± 0.9 (15)					−1.2 ± 0.009 (15)
2	0.4 ± 0.4 (11)	−0.3 ± 0.5 (14)	−1.8 ± 0.8 (9)	−4.1 ± 1.3 (3)		−0.7 + 0.4 (37)
3	−5.9[a] ± 0.8*** (14)	−0.4 ± 0.5 (25)	−1.8 ± 0.5** (17)	1.3 ± 0.6* (35)	−3.1 ± 0.9** (33)	−1.5 ± 0.4*** (124)
4	−2.1 ± 0.3*** (20)	−1.3 ± 0.3*** (28)	0.7 ± 0.5 (42)	0.9 ± 0.4* (30)		−0.2 + 0.2 (120)
5	−2.6 ± 0.3*** (23)	−5.4 ± 0.9*** (23)	−2.5 ± 0.5*** (24)	−2.2 ± 0.8* (19)	−4.6 ± 0.7*** (12)	−3.4 ± 0.3*** (101)
6	−4.7 ± 0.3*** (34)	−4.1 ± 0.4*** (43)	−5.2 ± 0.5*** (46)	−4.4 ± 0.5*** (32)		−4.6 ± 0.2*** (155)
7	−2.7 ± 0.2*** (24)	−2.0 ± 0.3*** (36)	−1.3 ± 0.4** (35)	−2.5 ± 0.3*** (45)	−0.4 ± 0.5 (21)	−1.9 ± 0.2*** (161)
All trips						−2.2 + 0.1*** (713)

[a] No ice used on this day of fishing. [b]$P<0.05$; **$P<0.01$; ***$P<0.001$.

Table 2

Summary of sampling trips, including trip length (d), total net landed catch (kg) and the estimated percentage of ice in the gross load (from processing plant records).

Trip	Trip length (d)	Total catch (kg)	Estimated percentage ice
1	1	600	35
2	4	7,900	16
3	5	15,000	17
4	4	11,900	23
5	5	5,200	32
6	4	25,200	7
7	5	14,000	11

val of 1.9% to 2.5% (Table 1). Four of the seven trips showed a statistically significant average weight loss ($P<0.05$), whereas three did not. None of the trips showed a gain in average weight of the shrimp samples, despite ice deductions as high as 35% of the gross load (Table 2).

The average weight change for samples from individual days and trips showed a large degree of variability. Several of the regressions of percent weight change versus elapsed time were statistically significant ($P<0.05$); however, the sign of the slope coefficient was inconsistent (Table 3). No consistent patterns were observed between average weight loss and trip length, total catch, or the percentage of ice in the load (Tables 1 and 2). The average weight loss observed in samples which had been on ice for only a short period of time (Table 1 and Figure 1), in combination with the significant positive slope of several of the regressions, suggests that commercially handled, iced pink shrimp generally lose some weight very shortly after capture, and, in many instances, slowly gain weight for some time afterwards. However, the one regression with a positive intercept and significant negative slope (Table 3, trip 2), in combination with the variability of average weight change (Table 1), demonstrate that weight change of shrimp under actual commercial handling and icing conditions is quite variable. The lack of a truly consistent pattern of weight change versus elapsed time suggests that Figure 1 may portray shrimp weight change under actual commercial fishing conditions as well as anything else presented.

Table 3

Summary of linear regression analysis of percent weight change on elapsed time for each trip and all trips combined. Model is Percent Weight Change = $a + b$ (Elapsed Time). NS = not significant.

Trip	Intercept	Coefficient	$P>F$
1	–0.207	0.013	0.0002
2	0.023	–0.001	0.0001
3	—	—	NS
4	–0.024	0.00041	0.0001
5	—	—	NS
6	—	—	NS
7	–0.027	0.00014	0.0238
All trips	–0.029	0.00013	0.00027

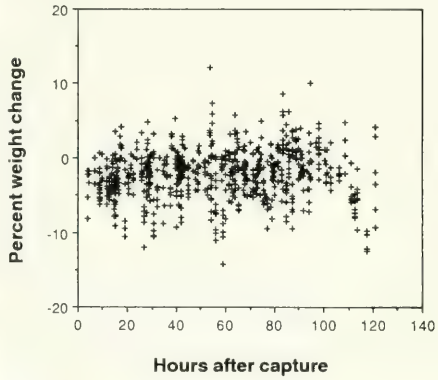

Figure 1

Percent weight change versus elapsed time from capture to unloading for samples of trawl caught pink shrimp ($N = 713$)

Interestingly, there were daily average weight change values which exhibited a significant positive change (Table 1), probably owing to absorption of meltwater from the ice. Samples from two trips showed large deviations from the average weight change which were readily explainable. On trip 3, the vessel ran out of ice on the final day of fishing, and, on trip 6, some spoilage was found throughout the load suggesting inadequate icing. In both cases the samples showed high weight loss values, 5.9% and 4.6% respectively.

These data suggest that there are small but fairly consistent losses in average weight of pink shrimp between commercial capture and unloading, at least when the shrimp are adequately iced. The results of this study appear to conflict with the findings of Bullard and Collins (1978), that iced *Pandalus borealis* gained 11% in weight in the first 1.5 days and maintained this gain for 8.5 days. However, the different methods used readily explain the different findings of the two studies. Bullard and Collins (1978) worked with shrimp which had been held at –1.7°C for two hours and then rinsed and drained for 30 minutes to produce stable weights prior to icing. The shrimp employed in this study were very fresh, sometimes jumping off the scales. If the average weight loss observed in this study occurs very rapidly, perhaps owing to loss of fluids just after the shrimp have died, or from the initial crush of the catch in the hold, such a loss could not have been detected in the Bullard and Collins (1978) experiment. It is not clear what percentage of ice was used by Bullard and Collins (1978), but they refer to it as "an excess of ice." Given the weight gain observed in some of the samples in this study, and the modest percentages of ice (Table 2), the results of the two studies are not inconsistent. Perhaps, however, the differences do suggest the importance of studying the weight change of shrimp under both laboratory and actual commercial fishing conditions.

An average weight loss of 2.2% from capture to unloading is sufficiently small as to be insignificant from a management standpoint. The minimum aggregate size limit of 353 shrimp per kg (160 shrimp per lb), which is intended to provide some protection from harvest for age-one shrimp, is based on average size-at-age data. Interannual and geographic variability in shrimp growth easily exceeds 2.2% (Hannah and Jones, 1991). The findings of this study are significant however, principally in that they demonstrate that the change in weight of pink shrimp that should be expected, when using normal icing procedures, is fairly small. Accordingly, fishermen can readily comply with the minimum size regulation.

Acknowledgment

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Occurrence and seasonal variations of spiny lobsters, *Panulirus argus* (Latreille), on the shelf outside Bahía de la Ascensión, México

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The spiny lobster, *Panulirus argus*, is one of the most valuable fishery resources on the Mexican Caribbean coast (Secretaría de Pesca, 1987). Lobsters are caught with traps and tangle nets, as well as by SCUBA diving, only on the shelf around Isla Mujeres and Isla Contoy (Fig. 1A), at significantly greater depths than elsewhere on the coast (Seijo et al. 1991). From Puerto Morelos to Xcalak, where the continental shelf is extremely narrow, lobsters are captured mainly by skin diving in the shallow coral reef and lagoon areas (Lozano-Alvarez et al. 1991a).

In Bahía de la Ascensión (Fig. 1B), the fishery for *P. argus* is based on the use of artificial shelters, called "casitas." Casitas are deployed on the bottom and the lobsters sheltering beneath them are caught by skin-diving fishermen. Both casitas and the fishing method are thoroughly described elsewhere (Lozano-Alvarez et al. 1989, 1991a; Briones et al. in press). Casitas are installed only within the bay, but some fishermen also skin dive for lobsters in the shallow coral reefs adjacent to the bay. No lobster fishing is conducted on the coastal shelf outside the bay deeper than 15 m. Only the tails are used. Tails are graded according to weight, packed in 10-pound (4.65 kg) boxes, and frozen. Fishing regulations include a minimum size limit of 13.5 cm tail length (≈74 mm carapace length, CL), a prohibition on the catching of egg-bearing females, and a closed season from 1 March to 30 June.

In 1985–87, results from a tagging program showed that the spiny lobster population within the bay comprised mostly juveniles and subadults (Lozano-Alvarez et al. 1991a). Growth of lobsters in the bay was fast, and they moved from the bay area towards the coral reefs as they grew. No evidence of reproductive activity in bay lobsters was found (Lozano-Alvarez et al. 1991a). Size of onset of sexual maturity is ≈80 mm CL, but females do not become fully mature until approximately 90 mm CL (Fonseca, 1990). This raised the hypothesis of the existence of the reproductive segment of the population on the shelf outside the coral reef, at greater, currently unfished depths. Lozano-Alvarez et al. (1991a) stressed the need to test this hypothesis for future management plans.

In this paper, we present evidence of the occurrence of adult reproductive *P. argus* on the continental shelf outside Bahía de la Ascensión, and discuss seasonal variations in abundance and some biological aspects of this segment of the population, as well as its potential importance as a refugium in space. The fisheries aspects of the study were published elsewhere (Lozano-Alvarez and Negrete-Soto, 1991).

Methods

Bahía de la Ascensión (Fig. 1B) is a large (≈740 km^2) and shallow (<6 m deep) bay, bordered by mangroves and grass swamps. A substantial part of the bottom of the bay is covered with seagrass (mainly *Thalassia testudinum*) and dense aggregations of red and green algae (Briones et al., in press). A coral reef tract exists along its mouth, protecting the inner waters of the bay from wave surge. The bay is a nursery area for *P. argus* (Lozano-Alvarez et al. 1991a).

Fishing operations for spiny lobsters were carried out on the continental shelf outside the coral reef tract (Fig. 1B) during two different seasons, summer (11 July–10 September 1989, six fishings), and winter (14 November 1989–27 February 1990, five fishings). Standard lobster traps of the kind used by fishermen at Isla Mujeres were set. The traps were rectangular, measuring 121 × 91 × 40 cm. The frame, built with 12-mm diameter rod, was covered with plastic coated galvanized wire mesh (5 × 2.5 cm), and an entrance was left on one of the small sides. Traps were baited with cow hide.

A maximum of 39 traps was installed in any fishing operation, in lines parallel to the coral reef. The continental shelf in front of the bay is narrow, not exceeding 4 km from the coast. Complex reefs exist in this area at depths of <10 m and from 30 to 40 m (Jordán-Dahlgren et al., in press). After 40 to 60 m the slope becomes very steep, rapidly reaching depths in excess of 400 m. Echosounding was used to

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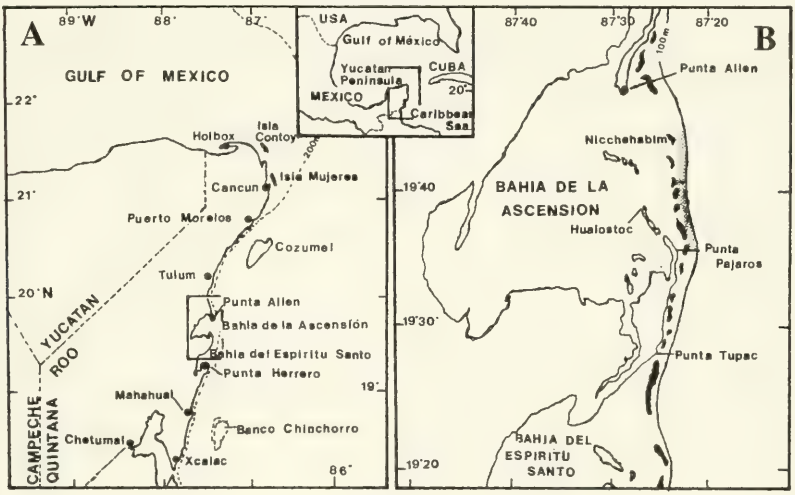

Figure 1

(**A**) The coast of Quintana Roo, showing the main fishing localities for *Panulirus argus*. (**B**) Bahía de la Ascensión. Black areas denote coral reef tracts; shaded areas show the sector of the shelf where exploratory fishings with traps were carried out. Casitas for lobster fishing were used coastward from the coral reef.

locate suitable bottoms for installing traps to minimize trap loss. In certain areas where the deep reefs are well developed (e.g., offshore from Punta Allen, Fig. 1B), no suitable bottoms were found. Thus, fishing operations were constrained to a range of depths between 15 and 30 m, from Nicchehabim Reef to Punta Pájaros (Fig. 1B).

Because soak time does not affect catch rate of the traps (Lozano-Alvarez et al., 1991b, Lozano-Alvarez and Negrete-Soto, 1991), we considered the number of lobsters per trap-lift as a gross index of abundance. Carapace length (CL) of lobsters was measured (±0.1 mm) from between the rostral horns to the posterior dorsal edge of the cephalotorax. Carapace state of lobsters was recorded following an arbitrary scale from 1 (newly molted and completely clean) to 4 (heavily fouled), as a relative indicator of the time elapsed since the last molt (Kanciruk and Herrnkind, 1976). Females were considered non-reproductive (NR) when eggs were absent, the carapace was clean, and no traces of spermatophores were found on the sternum. Reproductive females comprised those that presented a new spermatophore attached to the sternum (SP); external eggs attached to the pleopods (EE); or empty egg capsules remaining on the pleopods (EC).

To compare the size distribution and general features of the lobsters found on the shelf outside the bay with those from the bay, two different groups of data were obtained from the bay area. Throughout the fishing season, July 1989–February 1990, monthly data from a number of boxes of lobster tails, categorized by tail weight (TW, g) class, were obtained from a local processing plant. This plant receives all the catch from the bay area. The data were transformed to CL by applying the following equation: Log TW (g)= 2.550 log CL (mm) –2.69298 (Lozano-Alvarez et al., 1989). However, because the size structure of the catch is constrained by the minimum size limit and includes lobsters caught on the fore-reef down to a depth of 15 m, and the catch data gives no information on sex or reproductive activity, we also used data from Lozano-Alvarez et al. (1991a) taken during a tagging operation carried out in May–June 1986, which comprised lobsters found solely beneath casitas throughout the bay, as a less biased estimate of size structure, sex ratio, and carapace state of lobsters in the bay.

Student's *t*-test (Zar, 1984) was used to compare log-transformed data on seasonal abundance of lobsters (number of lobsters per trap-lift), mean sizes between males and females, and mean sizes between shelf and bay lobsters. Sex-ratios were compared with a χ^2 test. Mean sizes of summer and winter lobster catches taken on the shelf outside the bay were compared with a

Table 1

Number of traps lifted, number of lobsters (*Panulirus argus*) caught, and number of lobsters obtained per trap-lift during exploratory fishings with traps (summer 1989 and winter 1989–1990), on the continental shelf outside Bahía de la Ascensión, México.

Date of trap-lifting	No. of traps lifted	No. of lobsters	Lobsters per trap-lift
Summer			
Jul 19, 1989	36	0	0
Jul 24	21	16	0.76
Aug 10	18	23	1.28
Aug 16	13	5	0.38
Aug 22	34	14	0.41
Sep 05	34	9	0.26
Total summer	156	67	0.43
Winter			
Nov 23, 1989	39	106	2.72
Nov 26	30	29	0.97
Dec 05	39	204	5.23
Dec 08	13	21	1.62
Feb 27, 1990	39	35	0.90
Total winter	160	395	2.47

Table 2

Catch composition of *Panulirus argus* caught on the shelf outside Bahía de la Ascensión during the exploratory fishings with traps (summer 1989 and winter 1989–1990), and of those obtained from beneath casitas in the bay during May–June 1986 (M=males, F=females, CL=carapace length in mm).

	Offshore		
	Summer	Winter	Bay[a]
N	67	395	1402
Male: Female	1.31:1	1.04:1	1.04:1
Mean CL, F.	89.3	78.9	64.4
CL range, F.	55.0–156.9	52.4–117.2	22.0–100.3
Mean CL, M.	111.0	88.7	65.9
CL range, M.	76.5–162.1	56.0–134.0	29.8–113.1

[a] Data from Lozano-Alvarez et al. (1991a).

Table 3

Percentage of *Panulirus argus* in each of the four carapace states, caught on the shelf outside Bahía de la Ascensión during the exploratory fishings with traps (summer 1989 and winter 1989–1990), and of those obtained from beneath casitas in May–June 1986. Carapace states 1–4 represent a range from newly molted and completely clean to heavily fouled.

	Offshore		
Carapace state	Summer (*N*=67)	Winter (*N*=395)	Bay (*N*=1402)
1	35.82	74.43	55.99
2	37.31	18.99	37.44
3	17.91	6.07	6.13
4	8.95	0.50	0.42

non-parametric Mann-Whitney *U*-test with normal approximation (Zar, 1984). The level of significance considered throughout this paper is $P = 0.05$.

Results

Size structure and catch composition of lobsters on the shelf outside the bay

A total of 462 lobsters, 239 (52%) males and 223 (48%) females, were caught during fishing operations outside the bay. The observed sex ratio was not significantly different from the expected value (χ^2=0.554, df=1). Males were significantly larger than females (t=25.06, df=460, P<0.001). Mean CL for males was 92.2 mm (range: 56.0–162.1 mm) and for females was 80.4 mm (range: 52.4–156.9 mm).

Of the total catch obtained outside the bay, only 67 individuals (29 females and 38 males) were caught during the summer, while 395 (194 females and 201 males) were captured in the winter. Abundance of lobsters on the shelf outside the bay, expressed as number of lobsters per trap-lift, was significantly higher

Table 4

Reproductive state by size class of female *Panulirus argus* caught on the shelf outside Bahía de la Ascensión during exploratory fishings with traps (summer 1989 and winter 1989–1990). NR=non-reproductive; SP=new spermatophore on sternum; EE=external eggs on pleopods; EC= empty egg capsules on pleopods. Reproductive females comprise states SP, EE and EC.

Size class (CL, mm)	Summer				Winter			
	NR	SP	EE	EC	NR	SP	EE	EC
<80	8	0	0	0	112	0	0	0
80-85	3	1	1	0	21	0	1	6
85-90	1	1	0	1	27	1	0	4
90-95	5	0	0	1	1	2	0	5
95-100	0	0	0	1	2	0	0	3
100-105	0	0	0	2	1	0	0	2
105-110	0	0	0	1	1	2	0	0
110-115	1	0	1	0	0	0	0	1
>115	0	1	0	0	1	0	0	1
Total	18	3	2	6	166	5	1	22

during the winter than during the summer (t=4.21, df=9, P< 0.01) (Table 1). No significant differences in sex ratio were found between the two seasons (χ^2=1.332, df=1). The mean CL of the whole catch (Z=8.25, df=460, P<0.001), and of both males (Z=5.99, df=237, P< 0.001) and females (Z=4.15, df=222, P<0.001), was significantly greater in summer than in winter (Table 2).

Newly molted lobsters (carapace state 1) were more abundant in winter (74.4%) than in summer (35.8%), whereas lobsters with old, heavily fouled exoskeletons were more evident in summer (8.95%) than in winter (0.5%) (Table 3). During the summer, 11 (38%) of the 29 females were reproductive, while only 28 (14%) of the 194 females caught in winter were in this condition (Table 4). In both seasons, reproductive females measured over 80 mm CL, and most were in stage EC (Table 4). Only 2 females in summer and 1 in winter were actually carrying eggs (EE).

Size structure and catch composition of lobsters from casitas within the bay

The 1,402 lobsters caught beneath the casitas during May–June 1986 comprised 713 (51%) males and 688 (49%) females. No significant difference from unity was found in sex ratio. Mean CL of males (65.9 mm) was significantly larger (t=2.50, df= 1000, P<0.01) than that of females (64.4 mm) (Table 2, data from Lozano-Alvarez et al., 1991a). Most of the lobsters within the bay were in carapace states 1 and 2, i.e., recently molted (Table 3). Only five of the 688 females from within the bay were reproductive (stage EC), but these were among the largest in size (87.0–100.3 mm CL), and were found in sites close to the reef (Lozano-Alvarez et al. 1991a).

Comparison of size distribution between the shelf and bay segments of the population

Figure 2 shows the size distribution of a) the sample taken from casitas within the bay (modified from Lozano-Alvarez et al. 1991, a and b) the total sample taken on the shelf outside the bay. Both males and females were significantly larger on the shelf than in the bay (t=25.88, df=948, P<0.001 for males, and t=18.47, df=917, P<0.001 for females), but females composed a small proportion of shelf lobsters ≥90.0 mm CL (Fig. 2B).

Size structure of lobsters in the commercial catch from the bay and adjacent shallow reefs

Table 5 shows the monthly size distribution of the catch taken by the fishermen. Peak catches occurred in the 69.3–76.3 mm CL size class (which includes the minimum legal size) throughout the fishing season, except in July, where the peak was located in the 76.3–82.4 mm CL class. Lobsters ≥102.2 mm CL probably represented the catch from the adjacent shallow reefs, and represented a small proportion of the catch during most of the fishing season.

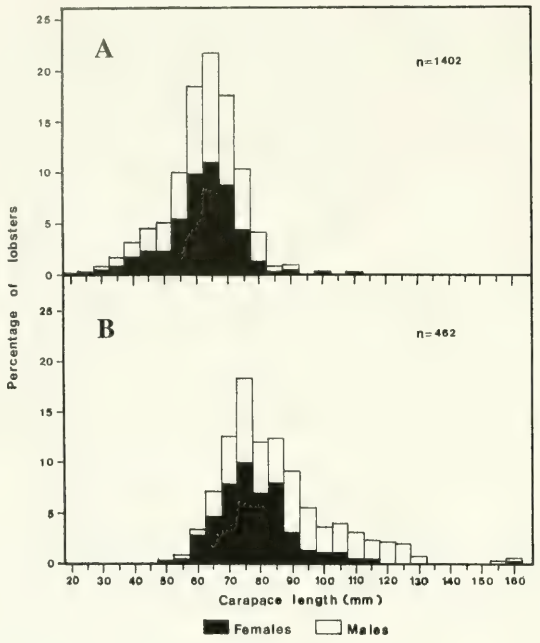

Figure 2

Size-frequency distribution of male and female *Panulirus argus* caught (**A**) beneath casitas within Bahía de la Ascensión (modified from Lozano et al. 1991a), and (**B**) in traps on the continental shelf outside the bay.

Discussion

The occurrence of a reproductive segment of the population of *Panulirus argus* on the shelf outside Bahía de la Ascensión has been documented in this study. The large sizes of lobsters and the evidence of mating and spawning activity on the continental shelf indicate that reproduction takes place in this deeper, unfished habitat, as opposed to the smaller sized, non-reproductive segment of the population within the bay.

Munro (1974) suggested that in coralline areas it is unlikely that the amount of shelter would be a limiting factor for spiny lobsters, but that this might be important in shelf areas with sparse coral cover. The deep and complex reef formations on the shelf outside Bahía de la Ascensión (Jordán-Dahlgren et al., in press) likely offer abundant natural shelters for *P. argus*. Lobsters are attracted to traps for refuge rather than for food (Heatwole et al., 1988), and traps apparently fail to adequately sample resident individuals (Herrnkind, 1980). Thus, the poor catches obtained during our summer fishings probably reflected the occupation of the available natural shelters by resident adult lobsters. The resident nature of these lobsters seems to be further supported by the large proportion of reproductive females and the high incidence of lobsters with fouled carapaces. The existence of resi-

Table 5

Monthly size-frequency distribution of the commercial catch (July 1989–March 1990) of *Panulirus argus* in Bahia de la Ascension, obtained by converting tail weight (TW, g) to carapace length (CL, mm)*.

Commercial category (TW, g)	Size range (CL,mm)	Number of lobsters							
		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
60–100	56.7–69.3	1,484	848	636	1,274	636	424	0	371
100–128	69.3–76.3	17,720	6,680	5,240	4,640	3,200	2,680	2,401	1,600
128–156	76.3–82.4	18,464	5,408	3,680	3,456	2,144	1,760	2,240	1,184
156–185	82.4–88.1	12,717	3,672	2,592	2,241	1,431	1,134	540	621
185–213	88.1–93.2	6,785	2,461	1,656	1,472	897	690	690	391
213–241	93.2–97.8	3,480	1,460	960	880	560	420	402	240
241–270	97.8–102.2	1,692	900	612	468	306	342	180	162
270–298	102.2–106.3	944	432	352	288	160	240	0	128
298–340	106.3–111.9	810	480	285	255	150	180	0	105
340–397	111.9–118.9	572	338	195	195	117	156	130	91
≥397	≥118.9	486	348	191	110	81	171	190	91
Total		65,154	23,027	16,399	15,279	9,682	8,197	6,773	4,984

* Log TW = 2.55 Log CL –2.69298 (Lozano-Alvarez et al., 1989).

dent populations of *P. argus* has been suggested in the Bahamas (Kanciruk and Herrnkind, 1978; Herrnkind and Lipcius, 1989) and the Dry Tortugas (Davis, 1974).

In contrast, the greater abundance of lobsters on the shelf during the winter, in addition to their smaller mean size and recently molted carapaces, indicates a recent recruitment of subadult lobsters to the deep habitat. The recruits likely originated in the bay, from where they exited in pulses, as suggested by the large number of lobsters caught in two fishings (Table 1). These two fishings were conducted immediately after the passage of two severe cold fronts. Offshore movements of *P. argus* associated with cold fronts have been documented in other parts of the Caribbean and Florida (Herrnkind, 1980). Moreover, catches increase notably in winter in the deep fishery off Isla Mujeres, whereas catches from more shallow areas, such as Bahía de la Ascensión and Banco Chinchorro (Fig. 1A) decline at that time of year (Lozano-Alvarez, 1992). However, lobsters moving along the coast (Davis, 1979; Gregory and Labisky, 1986; Fonteles-Filho and Corréa-Ivo, 1980; Herrnkind, 1980) could also account for the greater abundance found on the shelf. Some lobsters tagged in Bahía de la Ascensión were recovered at locations several kilometers to the north and south of the bay (Lozano-Alvarez et al. 1991a). The extent of these movements along the offshore depth contours remains unknown, and warrants further investigation.

In contrast to the sex-ratio in our shelf samples, females outnumbered males in offshore *P. argus* populations in Florida (Davis, 1974; Lyons et al., 1981; Hunt et al., 1991[1]). Although in the Mexican Caribbean the reproductive season spans from March to November, with significant peaks in August–September (Fuentes-Castellanos, 1988), fully mature females, particularly those bearing eggs, were very scarce in our shelf samples. However, considerable evidence exists suggesting that traps fail to sample gravid females in several species of spiny lobsters (Hèrrnkind, 1980). We believe that gravid females were underestimated in our shelf samples owing to the availability of natural shelter.

The distribution of lobsters in and outside Bahía de la Ascensión seems to conform to the known size-related distribution of *P. argus*, that is to say juveniles inhabite shallow habitats (lagoons, bays) and adults dwelling on deeper reef habitats. However, some large adult lobsters were found in the bay and shallow adjacent reefs (Fig. 2A, Table 5). This fact suggests that some adult lobsters return to inshore habitats after their ontogenetic migration to deeper habitats. Inshore movements of large *P. argus* have been documented in Antigua and Barbuda (Peacock, 1974), Brazil (Fonteles-Filho and Corréa-Ivo, 1980) and Florida (Gregory and Labisky, 1986; Hunt et al., 1991). Hunt et al. (1991) suggested that these inshore movements are controlled by changes in behavior associated with reproduction.

The *P. argus* population in Bahía de la Ascensión and adjacent offshore areas is highly dynamic. Fishing pressure on juveniles in the bay and near shallow reefs is heavy (Lozano-Alvarez, 1992), but the closed season is strictly observed, and no lobster fishing is conducted offshore. Developing an alternative trap fishery off Bahía de la Ascensión would be impractical and costly, because of the narrowness of the shelf, the complex morphology of the bottom, the strong currents encountered in the zone, and the small and variable CPUE of legal-sized lobsters obtained (Lozano-Alvarez and Negrete-Soto, 1991). Consequently, the fishery will continue to be focused on the small-sized lobsters in the shallow areas.

Despite heavy fishing in the bay, we found evidence of a winter offshore migration. Lozano-Alvarez (1992) estimated a high emigration rate from the bay throughout the year, so other offshore recruitment pulses may occur at other times of the year (e.g., the closed season). Because of their large sizes, the resident females on the shelf outside the bay have high indices of egg productivity (Fonseca, 1990), and spawn more than once in the reproductive season (Lipcius, 1986). Thus, the unfished deep habitat outside the bay may bear importance as a refugium in space (Campbell, 1989; Caddy, 1990) for reproductive lobsters.

Other deep, currently unfished lobster areas were found offshore from Puerto Morelos (Lozano-Alvarez et al., 1991b) and probably exist elsewhere along the coast of Quintana Roo, particularly on the narrow shelf from Puerto Morelos to Xcalak (see Fig. 1A), and in many other areas of the Caribbean as well (e.g. Cuba, González et al., 1990). Their existence might serve to mitigate, through the production of larvae, the pressure exerted on more heavily fished stocks. We propose that the deep habitats on the shelf outside Bahía de la Ascensión should be left undisturbed as a nucleus of protected spawning stock, regardless of the unknown final destination of the larvae. We similarly encourage the protection of other deep, currently unfished areas throughout the Caribbean, as a means to preserve groups of reproductive lobsters that contribute larvae to the regional pool.

[1] Hunt, J. H., T. R. Matthews, D. Forcucci, B. S. Hedin, and R. D. Bertelsen. 1991. Management implications of trends in the population dynamics of the Caribbean spiny lobster, *Panulirus argus*, at Looe Key National Marine Sanctuary. Final Rep., NOAA Office of Ocean and Coastal Resource Management, Sanctuary Programs Div., Contract 50-DGNC-6-00093, 81 p.

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Growth and maturation of winter flounder, *Pleuronectes americanus*, in Massachusetts

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Winter flounder, *Pleuronectes americanus*, is an important commercial and recreational species along the Atlantic coast. Previous studies have shown that the winter flounder stock is composed of several substocks that may consist of estuarine specific populations (Saila, 1961; Poole, 1966a; Pierce and Howe, 1977). Coastal stocks of winter flounder are managed by individual states; area specific growth and maturity information is incorporated into spawning stock biomass-per-recruit models (ASMFC, 1992).

For management purposes, two stocks of winter flounder inhabit Massachusetts waters; one stock north of Cape Cod and the other stock south and east of Cape Cod (Lux et al., 1970; Howe and Coates, 1975; Pierce and Howe, 1977). For these stock units, growth parameters and sex ratios were reported from 1964 to 1968 coastal tag returns (Howe and Coates, 1975), but no studies using aged scale or otolith samples had been undertaken. Growth rates estimated from tagging may not be equivalent to those based on age-length data (Francis, 1988). The two methods often provide different results; faster growth rates are generally estimated from tag returns.

The primary objective of our study was to determine growth rates of juvenile and adult winter flounder based on aged scale samples. Our second objective was to determine average maturity schedules for the two winter flounder stock units, as maturation is an important life history parameter for spawning stock biomass-per-recruit analyses.

Materials and methods

Winter flounder were sampled during the 1983–91 Massachusetts Division of Marine Fisheries spring (May) bottom trawl surveys. State waters (0–3 mi) were surveyed with an otter trawl equipped with a fine mesh (13-mm stretch) codend liner that retained small fish. An average of 95 stations per year were surveyed in a stratified random manner, at a sampling intensity of 1 station per 19 square nautical miles. Additional details of trawl survey methodology were provided by Howe (1989). Captured winter flounder were measured to total length (±0.5 cm), sampled for scales and otoliths, and assigned sex and maturity stage based on examination of the gonads, by using established macroscopic criteria (Burnett et al., 1989). Because samples were collected at the end of the winter flounder spawning season, determination of sex and maturity stage was relatively straightforward. Scale samples, taken from the caudal peduncle region, were used for age determination. Scales were impressed in acetate and aged as described for Georges Bank winter flounder (Fields, 1988).

Von Bertalanffy growth curves were fitted to length-at-age data (1983–91 pooled) for males and females of each stock unit, by using mean lengths observed for ages 2–8. Data from age-1 fish were not included, as preliminary analysis suggested that the smaller fish of this age group were either not available or not effectively captured by the sampling gear. Mean lengths at age for older (>8 yrs) fish were not used in fitting growth models, because sample sizes were small. Statistical comparison of the results from this study and those of Howe and Coates (1975) was not attempted, as growth parameters derived from tagging and age-length information may not be equivalent (Francis, 1988).

Stock-specific maturity schedules based on aged fish were calculated for both males and females. For each sex within each stock unit, a logistic function was fitted to the proportion of mature winter flounder, ages 2–5, by using nonlinear regression. Lengths at 50% maturity (L_{50}) were the inflection point on these curves. Similarly, ages at 50% maturity (A_{50}) were determined from logistic curves fitted to observed maturity at age data.

Results

A total of 3,035 winter flounder (731 males and 986 females south and east of Cape Cod and 509 male and 809 female winter flounder north of

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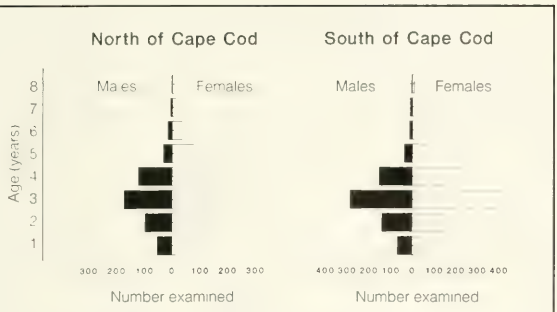

Figure 1

Sample sizes of male and female winter flounder taken from each stock area, 1983–91.

Cape Cod) were successfully aged and assigned maturity stages. Ages ranged from 1 to 16 years in the southern stock, and 1 to 15 years in the northern stock. For both stocks, females predominated at ages 3 and older (Fig. 1).

Growth rates of winter flounder differed for each gender and stock unit. Females grew faster than males, and obtained larger mean asymptotic lengths (Fig. 2). For each gender, winter flounder from the southern stock were generally larger at age than those from the northern stock, at ages 3–8. Mean lengths at age observed from our samples were similar to, but slightly smaller than, those determined from 1964–68 tag return data (Table 1).

For both stocks and sexes, maturation generally began at age 3 and was nearly complete at age 5. Maturation of age-3 and age-4 fish was quite variable and was somewhat sensitive to size at age (Fig. 3). Owing to their somewhat faster growth rate, winter flounder matured at younger ages south of Cape Cod. For females, A_{50}'s (and corresponding L_{50}'s) were 3.0 years (28.3 cm) south of Cape Cod and 3.3 years (28.7 cm) north of Cape Cod. For males, A_{50}'s (and corresponding L_{50}'s) were 3.1 years (28 cm) south of Cape Cod and 3.3 years (27.2 cm) north of Cape Cod.

Discussion

Adult winter flounder south and east of Cape Cod were larger at age than adults from other coastal populations. For example, age-5 female winter flounder in

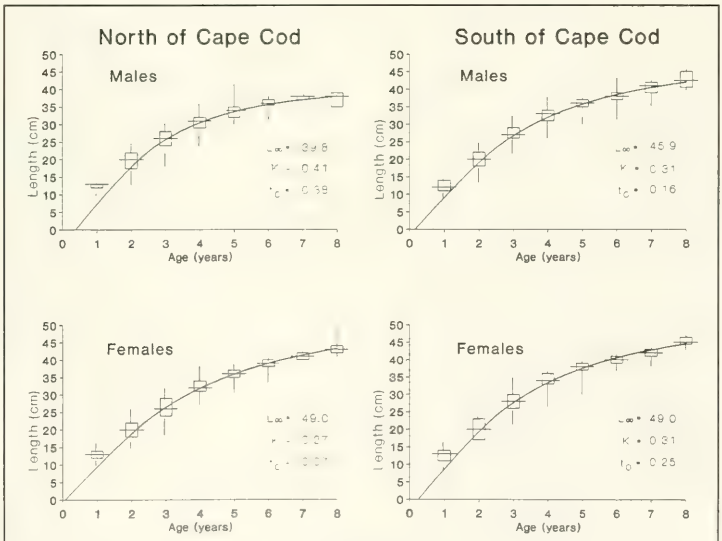

Figure 2

Distributions of length at age for male and female winter flounder sampled from both stock units. Von Bertalanffy growth curves are fitted through mean lengths, ages 2-8. Box plots of the median, quartiles, and range of lengths at age are shown.

Table 1

Calculated total length (cm) at age (yr) for female winter flounder in Massachusetts from 1983–91 scale samples (present study) and from 1964–68 tag returns (Howe and Coates, 1975).

	North of Cape Cod		South of Cape Cod	
Age	1964–68	1983–91	1964–68	1983–91
2	—	19.9	—	20.5
3	29.0	26.8	29.4	28.1
4	34.1	32.0	35.0	33.6
5	37.6	36.1	39.0	37.7
6	40.1	39.1	41.8	40.7
7	41.8	41.4	43.8	42.9
8	43.0	43.2	45.2	44.6

Massachusetts averaged 38 cm south and east of Cape Cod, versus 36 cm north of Cape Cod, 21 cm in Long Pond, Newfoundland (Kennedy and Steele, 1971), and 35 cm in Narragansett Bay, Rhode Island (Berry et al., 1965). On Long Island, New York, Poole (1966a) found that growth rates of winter flounder increased from south to north; age-5 females ranged from an average of 31 cm in Great South Bay to 36 cm in Peconic Bay. Only the offshore population on Georges Bank is known to have faster growth rates than winter flounder in Massachusetts waters south and east of Cape Cod (Lux, 1973; Howe and Coates, 1975). The area south of Cape Cod is the center of the species geographical range (ASMFC, 1992) and may provide better environmental conditions for growth of winter flounder than other coastal areas.

For both stocks of winter flounder in Massachusetts, growth was apparently not affected by changes in exploitation or biomass. Biomass of these stocks declined over 50% from 1983 to 1990 owing to high fishing mortality (Howe et al., 1990). However, no trends in mean lengths at age were observed for the 1983–91 period, and growth rates were similar to those observed by Howe and Coates (1975) for the 1964–68 period (Table 1), when winter flounder were more abundant and exploitation rates were lower[1]. Under high levels of exploitation, faster growing fish are differen-

[1] Foster, K. L. 1987. Status of winter flounder (*Pseudopleuronectes americanus*) stocks in the Gulf of Maine, southern New England, and middle Atlantic areas. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 87–06.

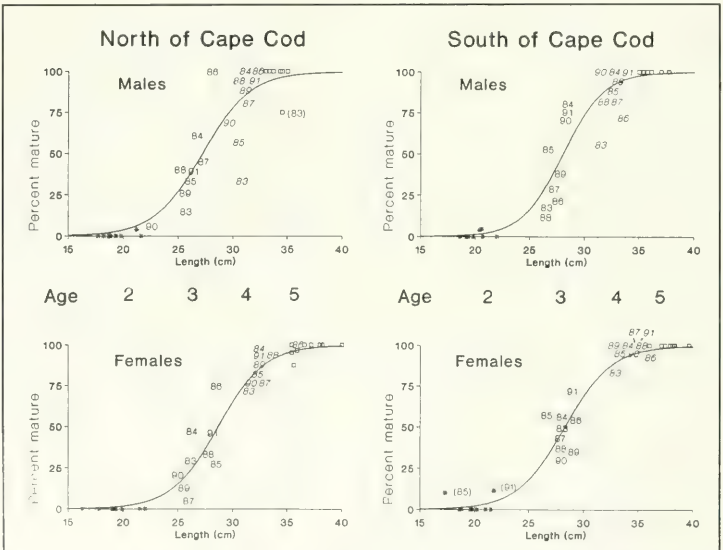

Figure 3

Variability in maturity and mean length at age for winter flounder, ages 2-5, observed from 1983–91 bottom trawl surveys. Percent mature at length of age-3 and age-4 fish are plotted by year of collection (age-4 fish shown in italics). Data for age-2 and age-5 fish are plotted by stars and squares, respectively; outliers are identified by year of collection in parenthesis.

tially removed from populations (Ricker, 1975), and thus we were unable to separate the effects of cropping faster growing fish from potential density dependent effects.

Winter flounder in Massachusetts waters mature at larger sizes than winter flounder from other coastal populations. For winter flounder in Massachusetts, only 50% of the females were mature at 28 to 29 cm; L_{50}'s of females in Newfoundland were 25 cm (Kennedy and Steele, 1971) and 27 cm in New Jersey (Danilla, 1978). Maturity ogives derived from our age-specific mean length at maturity data were similar to those reported from pooled length at maturity observations for Massachusetts winter flounder during the period 1985–89 (O'Brien et al., 1993). They found lengths at 50% maturity of females to be 27.6 cm south of Cape Cod and 29.7 cm north of Cape Cod. Because populations of long lived, late maturing fish are more susceptible to overexploitation than are populations with early maturity and shorter life spans (Pitcher and Hart, 1982), each substock of winter flounder may require different management strategies (including size limits) for optimal harvest levels.

Sex ratios of winter flounder favored females at older ages (Fig. 1), indicating a higher natural mortality rate for males. An increasing proportion of females by size was observed for winter flounder in Rhode Island, but the differences in sex ratios were thought to be related to the faster growth of females (Berry et al., 1965). Female winter flounder on Georges Bank live longer than males (Lux, 1973). A number of mature male winter flounder in Conception Bay, Newfoundland, failed to produce gametes, and there was a trend towards an increasing proportion of nonreproductive individuals with advancing age, leading to the possibility that males enter senescence at younger ages than do females, and thus have a higher natural mortality rate (Burton and Idler, 1984). A higher natural mortality rate for males has been found for other flounders, including European plaice, *Pleuronectes platessa*, (Bidder, 1925) and summer flounder, *Paralichthys dentatus*, (Poole, 1966b), and it may be a general pattern that male flounders have shorter life spans than females.

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